

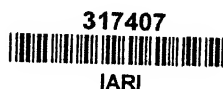


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Choice and Responsibility

BY

ALEXANDER PETRUNKEVITCH

(Address given at the Annual Meeting of the Connecticut Academy of Arts and Sciences, October 24th, 1946, on the occasion of his retirement from office as President of the Academy.)



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CHOICE AND RESPONSIBILITY

ALEXANDER PETRUNKEVITCH.

(ADDRESS GIVEN AT THE ANNUAL MEETING OF THE CONNECTICUT ACADEMY OF ARTS AND SCIENCES, OCTOBER 24TH, 1946, ON THE OCCASION OF HIS RETIREMENT FROM OFFICE AS PRESIDENT OF THE ACADEMY.)

Few problems can claim greater need of careful reconsideration on the part of men of science than those of choice and responsibility. Every human being in every walk of life, however exalted or humble, is daily making use of his inherent ability to choose under various circumstances. Occasionally one is even confronted with the necessity to make a decision which may affect one's entire future. Individually and collectively as associations and even as whole nations we are also aware of our obligation to live up to certain universally recognized moral principles and of our responsibility before existing laws, whether we approve of them or not. In case of disagreement between law and justice, as we commonly understand it, we seek justification of our actions in their being in harmony with some fundamental principles of either our religion or our philosophy of ethics. Such an attitude is natural, for regardless of scientific principles we all know that we possess the ability to choose. This is clearly reflected in the laws of all civilized nations, which distinguish between accident, negligence and willful action and appraise accordingly the legal responsibility. Thus in case of negligence the law usually assumes that a person charged with it *could* have acted in a way different from that in which he did act, if only he had paid attention to the circumstances and weighed in his mind the possible consequences of their disregard. In case of willful action the law further considers the question of whether the action was premeditated or the result of an impulse under great provocation. In special cases, when the sanity of the accused is in doubt, a criminal is subjected to an examination by psychiatrists with the object of determining the condition of his mind and thus to decide whether he understands

the difference between right and wrong. Here the law draws a distinction between an action which is not under control of the mind and one which could have been directed, granted the mind was sound. In other words the law assumes implicitly the possibility of choice, attributes responsibility only to a sound mind and does not lose itself in abstruse philosophy concerned with the problem of free will.

Not so the man of science. In his daily life, including also the routine of teaching and research, he does not differ from the average person and has often to make a choice between various possibilities by which he is confronted, a choice governed by circumstances and by the logic of his mind. But unlike the average person or the lawyer, when asked whether his choice was activated by his free will, the man of science will almost certainly answer: "Of course not! There is no such thing as free will. All our actions are determined." If then you ask: "But how about the Uncertainty Principle recognized by modern physicists?" he will reply: "That principle applies only to ultra-microscopic things. The larger bodies are subject to strict statistical laws which permit exact prediction of their behavior, and human beings form no exception." The modern biologist remains a determinist. Physical science has given up the law of causality, as that law was understood in the past centuries before the establishment of the Uncertainty Principle. It has admitted the existence of diverse possibilities and has applied the laws of chance and probability to physical phenomena. Some scientists ventured to draw a distinction between inanimate objects and living beings in regard to the second law of thermodynamics, which according to them is not applicable to the latter. But here any further attempt at distinction stops, partly because of an objection on the part of biologists to an admission of any fundamental difference between the operation of forces in living organisms and in inanimate objects, partly because of the survival of the old idea that "free will" means action without cause. To show the fallacy of such reasoning we must consider the problem from a new point of view which I will try to develop here.

The old law of causality postulated that every cause has its effect, that cause and effect are bound to each other by inexorable necessity, that the same cause can produce only the same effect

and that therefore not only the exact position of any body in space in a given moment of time, but also any event whatsoever can be predicted if all causes are known. That idea formed the foundation of Laplace's cosmogony and led him to the conclusion that "this axiom, known under the name of the principle of sufficient reason applies even to the most insignificant acts. These the freest will could not possibly produce without a determining motive, for if, all circumstances in two situations being identical, in the one it should act and in the other abstain from acting, its choice would be an effect without a cause." Heisenberg in creating his celebrated Uncertainty Principle did not set aside the philosophic principle of sufficient reason. He only showed that the exact position of an electron at a given moment of time cannot be determined with certainty. Discussing the principle in a more popular book "Matter and Light" published in an English translation in 1939, the distinguished French scientist De Broglie explains the situation in the following words: "The more exactly we wish to determine the position, the less exactly will the motion be determined. Conversely, the more exactly the motion of the corpuscle is defined, the more closely will the associated wave approximate to a plane monochromatic wave of constant amplitude. Hence the more exactly the state of motion is defined, the less exactly will it be possible to define the position of the corpuscle." (p. 188.) In this case Planck's quantum constant h and the length of a wave of rays of light used for the measurement are responsible for the uncertainty. The same condition applies to other phenomena. "Thus in every physical phenomenon there remains a margin of uncertainty; and it is possible to ascertain that this margin of uncertainty is measured, in a way, by the constant h ." (ibid. p. 246.) This condition, however, applies only to very small particles. We must "remember the minuteness of the constant h relatively to the magnitudes operating in mechanical phenomena on the human, and *a fortiori* on the astronomical scale Hence there is an *apparent* Determinism in macroscopic phenomena, which in no way conflicts with a certain indeterminateness in phenomena on the microscopic scale." (ibid., p. 247.)

In the same book, in the chapter "Philosophical studies on Quantum physics" De Broglie writes: "We may thus consider the corpuscle "free," in a sense, to manifest itself at a variety of

different places with an energy which may also vary; but, given the initial data, we can calculate *exactly* the probability that it will choose certain values and positions rather than others If we take macroscopic phenomena in whose case classical Mechanics can give exact figures, and calculate numerically the essential degree of indeterminateness introduced by the new ideas, we shall find that the latter is invariably very much smaller than the accidental indeterminateness due to the lack of accuracy in the measuring instruments. In these circumstances, the essential indeterminateness is completely masked by the errors introduced in the course of experiment, and everything happens therefore as though it did not exist at all. In other words, each corpuscle at each of its manifestations has always, so to speak, to make the choice between several possibilities; but the limits of this choice are supposed to be so narrow that in practice, as also in experiment, everything happens as though instead of a free choice there were a strict determinism. Thus the *apparent* Determinism of large-scale phenomena by no means contradicts the ideas of new Mechanics." (p. 230.) The expression "free" used by De Broglie in quotation marks in the above passage and his statement that the corpuscle will *choose* certain values are of course only figurative. The stress of the argument is on the existence of *several possibilities* as to the place in which a corpuscle may be present at a given moment, not *a single possibility* as is inherent in the old law of causality. This abstract idea of the existence of several possibilities in any physical event was conceived by me independently, on philosophical grounds, and in a somewhat different form, twenty years before the establishment of the Uncertainty Principle by Heisenberg, when in a paper on the Freedom of the Will, published in 1906, I formulated my *Principle of Plural Effects* according to which "every cause is potentially capable of producing several effects." At that time I tried to explain my thought by reference to simple mathematical equations for which more than one answer may be found. I think now that the Principle of Plural Effects should be widened by giving it the following new definition: "*Every cause has potentially an infinity of effects.*" To explain this let us consider the simplest case, that of the displacement of a particle A at a given time from a point X to a point Z in space. We can imagine space as a sphere of endless dimensions, in which

the particle A represents the center and is surrounded on all sides by innumerable other particles. Now by changing its position from X to Z the particle A has changed its position not only in relation to point X which it formerly occupied, but to all other points of the infinite space and therefore in relation to every one of the infinite number of particles. If the particle A impinged upon a particle B at the point Z we disregard all other effects and speak of cause and effect only as related to the two particles A and B. In the world of physical forces distance would be a powerful limiting factor. Yet, if a simultaneous effect of any kind on particle C could be observed as due to the displacement of the particle A from the point X to Z, we would have to refer the effect on particle C to the same cause. The same reasoning applies to any phenomenon involving displacement in space. But the example shows only that a particle moving from one place to another changed at the same time its relative position in respect to all other particles. It does not show that the particle in question could have moved into some other place than point Z, regardless of the forces acting upon it. But the existence of an infinity of causes and effects at any imaginary moment is responsible for the limitation of the number of appreciable effects. The uncertainty of position can be therefore logically referred to the impossibility of applying any measurement in case of a problem involving infinity, because all measurement, by its very nature, is an attribute of limitation. In practice alternative possibilities may not be many, but they are the logical result of the interplay of an infinity of causes.

The presence of two or more alternative possibilities is, of course, prerequisite for choice in the common meaning of that word. It is also prerequisite for the operation of chance in accordance with the laws of probability. It is, therefore, necessary to draw a very clear distinction between chance and choice in order to avoid the pitfall of attributing an action of simple chance to a selection of one of the possibilities by an action of choice. Chance governs the physical world of inanimate nature. Perception of the existence of various possibilities is not required and does not enter into its operation. A torrent of water on reaching a bifurcation in its course in the bed of a dry creek will either divide into two currents or remain single and follow one of the channels, depending upon the chance distribution of obstructions, the speed

of its current, the quantity of water, etc. On the other hand a man at a crossroads may also proceed on the one or the other branch of the road leaving the decision to mere chance, such as when he has not perceived the existence of the bifurcation owing to darkness or because he was paying no attention to the road. Even if his senses were alert and he became aware of the bifurcation, he yet may leave the decision to pure chance by tossing a coin. Nor would his selection be due to choice if he were forced to do so by the existence of an obstruction in the road, or in order to avoid collision with a suddenly appearing moving vehicle. Granted normal conditions and a desire to select the road best suited to his purposes, the man will consult a map and use the acquired information to make a proper decision. But even in such cases of conscious, deliberate choice a man may be unable to do what he believes to be the correct thing to do, because, for example, he is physically incapable of doing it. Thus a man trapped in a room by fire making escape through the door impossible may know perfectly well that in such an emergency he should use the fire-escape, but cannot do so because he is a cripple, or because, as it happens so often owing to the negligence of others, there is no fire-escape available. An action based on choice, then, requires 1) perception of existing alternatives, 2) mental evaluation of each alternative, 3) decision in favor of one of them and 4) translation of the decision into action. There is no "insufficient reason" here for any action. The action is caused by the nervous impulse transmitted when the decision has been made after a mental evaluation of the alternatives, while the process of evaluation is itself consequent to the perception of existing possibilities. To imagine that human actions, because of the size of our body which greatly exceeds that of the Quantum constant \hbar , are determined by statistical laws of probability identical with those which govern such physical phenomena as the motion of celestial bodies, would mean a reduction *ad absurdum* of the function of our mind. Would it not be humiliating to be told, for example, that the decision to relay traffic in case of a railroad accident when the road is blocked by wreckage and the very process of working out a temporary, new schedule are predetermined by such laws and not in any way the result of careful consideration of all factors entering into the preparation of a workable time-table? And how about the forestalling

of a willfully planned crime or the winning of a battle by outwitting a shrewd enemy through the use of information which was not accessible to him?

We can, then, give to the old term "Freedom of the Will" a new and perfectly scientific definition. It is *the ability to translate into action the choice between alternatives*. Only the presence of alternatives makes choice possible. The choice is "free" inasmuch as it is a mental process deciding in favor of this or that alternative. But the final action is not "without cause," inasmuch as it is the result of a nervous impulse caused by a mental process induced, in its turn, by perception of alternatives.

The reason why inanimate objects obey only mechanical laws, while living organisms, at least such as possess a central nervous system may also exert choice and thus set aside the action of the statistical laws of probability, lies in the fact that the ability to perceive, to choose and to translate the choice into action are qualities inherent only in life. The old-fashioned mechanists used to deny any difference between living and dead matter and tried to explain the phenomena of life by forces operating in the physical world. They accused the old-fashioned vitalists of blocking the progress of science by postulating a special "vital force" operating only in living organisms and subject to its own laws, instead of subjecting each individual case to analysis by experimental methods used in physics and chemistry. Forced to admit the Uncertainty Principle as developed by the physicists, the new mechanists among the biologists persist in their method of approach to the solution of all problems of life. Along with the physicists they restrict the operation of the Uncertainty Principle to microscopic particles. They remain determinists in the case of macroscopic objects and try to explain the phenomena of life by the application to them of statistical laws of chance and probability. But the tables are turned now. Under the conception of plurality of effects as developed here, with an infinity of causes and an infinity of possible effects, uncertainty is operative in the case of higher living animals whenever choice becomes possible owing to the presence of alternatives and the ability to perceive them. There is a remarkable analogy between the behavior of microscopic particles and that of living beings, between the uncertainty in the position and momentum of an electron and the free choice of an alternative by an animal endowed with a mind. As De Broglie

stated, the more exactly we wish to determine the position of an electron, the less exactly will the motion be defined. C. G. Darwin in his book *The New Conceptions of Matter*, published in 1931, says on page 104: "There is also an Uncertainty Principle for the energy, just as there is for the momentum. This asserts that if we want to measure energy accurately we must take a long time in order to do so. If, on the other hand, we want to know the energy at a certain moment, we must obviously use a short interval of time round that moment to do the measurement, and the value we obtain will be inaccurate." On page 116 he says: "It is not by any means easy always to detect the fallacy in experiments like this, but there always is something wrong. Each time we find the defect in our process, we must install some extra piece of apparatus to put it right, and the addition, in the course of overcoming the old difficulty, always introduces a new one. There is no escape from the Uncertainty Principle." And on page 182 he says: "It is meaningless ever to ask what has happened, unless there is either a direct or an indirect observation to tell one; and if there is an observation, it is pointless to ask, because one knows the answer. The new mechanics represents the perfect antithesis to mysticism, for it denies sense to any question, unless we can verify the answer by an observation."

Now in the case of choice, translation of the mental process into action is possible only when there is no physical cause operative at that time, which is great enough to make the realization of the choice impossible. The experimental introduction of a new factor, that is of a new cause, which would make the selection of the same alternative inescapable and predictable, would not prove that choice as such is never possible, but merely demonstrate the relatively great impeding force of the experimentally introduced new cause. If, on the other hand, we attempted to make all involved factors in a series of experiments as nearly identical as possible in order to ascertain whether under such circumstances selection between the two alternatives would follow the one to one ratio of chance, we would find it impossible to demonstrate that the subject is capable to perceive the existence of an alternative. And in the case there were a difference in the ratio of selections of the A and B alternatives, our attempt to explain the difference on the basis of chance would be frustrated by the impossibility to demonstrate that no cause has been overlooked. There seems to be no way in which the impossi-

bility of free choice as defined here, can be disproved. The burden of proof that there is no difference between living beings and inanimate objects in the matter of choice lies on the shoulders of those who deny the existence of such difference.

The proof of its existence, however, is also impossible by other methods than reference to daily experience and logical conclusion. There is at least one similar case, the case of our own existence, which served as a bone of contention between philosophers of two different camps in the past, until the great Descartes settled the controversy by his celebrated imperative dictum *Cogito, ergo sum*—*I think, therefore I am*. In a similar manner, now that the old law of causality has been given up by the physicists and the Uncertainty Principle has taken its place, and in the light of the Principle of the Plurality of Effects as presented here, we may crystallize our conception of Free Will by saying: *Eligo, ergo possum*—*I choose, therefore I can*.

Heisenberg's Uncertainty Principle does not set aside a causal relationship between the past and the future position of an electron. As C. G. Darwin puts it on page 117 of his book already referred to, "the Uncertainty Principle is essentially only concerned with the future; we can install instruments which will tell us as much about the past as we like." Neither does the concept of free choice as based on my Principle of Plural Effects deny causal relationship between the act of choosing and the translation into action of the alternative which was chosen. What the concept of free choice asserts is that in presence of several alternatives the prediction of the choice is impossible as long as there is no cause present which is great enough to limit the choice or to make it altogether inoperative. The choice itself is assumed to be possible because of the inherent ability to perceive the presence of alternatives, an ability restricted to the operation of a conscious mind which itself is characteristic of only living organisms. That is *why* physical bodies are subject only to statistical laws and *why* the larger the bodies are, the stricter the determinism of their motion is, while in the case of a conscious mind aware of alternatives the laws of probability become less and less operative as the evaluation of the alternatives grows with their perception. That is *why* a rolling stone is controlled in its progress only by its size, mass, shape, momentum, friction, air resistance, etc. and crosses a road regardless

of traffic or traffic signals, while a man can choose the moment for crossing when traffic becomes less congested or when he sees the green light. That is *why* chemicals enter into certain definite reactions when brought together, while the experimenter can choose which chemical to put into the beaker and in which sequence. That is *why* rivers stay in their beds and torrents break improperly built dams, erode the soil and waste the water, while good dams hold the water and irrigation channels carry it to where it is needed. That is *why* man can plan for the future, can regulate the departure and the arrival of trains, can make and repeal laws. And that is *why* the question of responsibility arises in the case of man.

Clearly, responsibility has no meaning whatsoever where choice is impossible. In this respect the new mechanics of the physicists of today does not differ from the old mechanics of Laplace and the statistical laws of probability are as exacting as the inexorable law of causality. The motion of the planets is as strictly determined and their position in the sky may be predicted for years in advance. Thus C. G. Darwin is led to the following conclusion: "If an experiment is carried out with a thousand electrons, what was a probability for one, becomes nearly a certainty. Physical theory confidently predicts that the millions of millions of electrons in our bodies will behave even more regularly, and that to find a case of noticeable departure from the average we should have to wait for a time quite fantastically longer than the estimated age of the universe. How then does the Uncertainty Principle help to free us from the bonds of determinism?" (page 119). Now if that were true, then indeed each of our actions would have to be considered as determined and not as subject to choice. Assessing responsibility from this point of view, the best we could do would be to regard certain actions as undesirable and blame not an individual or a nation, but the configuration of physical causes that brought about these actions. Even so, we would have to find a criterion for the undesirability of such actions. To make a distinction in responsibility on the basis of sanity or insanity of the person who committed an undesirable act would be quite beside the point: neither the insane, nor the sane man could have prevented the consummation of the act. A difference in punishment would be in itself an act of unjustifiable distinction. Elimination of the possibility of a repetition of an undesirable action either through incarceration for life or by painless killing would be

the only reasonable way of dealing with the situation, since effectiveness of any other punishment depends on the ability of a person not only to learn by experience, but to be able to control his actions in another similar situation. Moreover, the basis for considering an action objectionable would have to be strictly utilitarian and the code of ethics simply a register of actions advantageous for the survival of the fittest. Indeed, that is what determinists maintain, because they deny the possibility of free choice, deny distinction between animate and inanimate nature and apply the same standards to both.

Those who like myself believe in a fundamental difference between living and dead matter are confronted with quite different difficulties which nevertheless are of a very serious nature. If we believe in the possibility of free choice, as indeed, I think, we *must*, then the choice is the cause of its consequences, and if the choice is based on an evaluation of perceived alternatives, then a sane individual is certainly responsible for it with all that it involves. But what is the standard of comparison? Responsibility before law is practical and is harped upon even to the logically ridiculous assertion that ignorance of the law is no excuse. In cases of injury or damage, compensation of the claimant is certainly justified even if the person responsible was not familiar with the law, but that is strictly legal responsibility and not one having to do with a conscious act of choice. As to law itself, it is after all man-made. Some law is good and some is bad. Some is at variance with the spirit of the times and some even with the professed religion of the law-makers themselves. Thus according to newspaper reports only a few weeks ago in the second half of the year of our Grace 1946, in the Christian State of Massachusetts the mayor of Taunton was sentenced to prison for cohabitation with a woman to whom he was not married, although the judge who pronounced the verdict in accordance with the existing law must have known his Bible well enough to remember that Christ said to the adulteress: "Neither do I condemn thee: go, and sin no more." (John 8.) And during prohibition in America several people were sentenced to prison for life because of their fourth offense which consisted in carrying a flask of whisky in their hip-pocket! Presumably the mayor of Taunton was acquainted with the archaic law of Massachusetts, applicable to his case. Certainly the men caught with the whisky flask in their hip-pocket

knew that they were breaking the prohibition law and were therefore legally responsible for their action. But from a common, human point of view the law invoked was responsible for a much more serious injustice than the poor devils who by their illegal action did no appreciable harm to anybody. Similarly, killing by an individual, except in self defense, is subject to heavy punishment, but the state does it when it inflicts capital punishment and does not treat the executioner as a criminal, but pays for his services. And in case of war, killing is wholesale and obligatory, and refusal to kill is a very serious offense. It is true that strictly offensive war finds now-a-days no supporters, but defensive war is still only too common and we are constantly reminded by the military that offensive operations are the best defense. Even Christian clergy finds excuses for killing in war, which shows, to say the least, that the justification of an action depends on the values one puts on alternative possibilities.

If we are to avoid the pitfall of utilitarian standard of ethics, such as determinists have perforce to adopt, we must refer our actions to some standard of universal value and not to one which may be applicable to a single nation because of the advantages derived from it by that nation. In religion and philosophy such a standard is inherent in the concept of God as a perfect principle. But I think that it is possible to find an absolute principle in nature without recourse to a concept of a divine power for the explanation of the mechanism of the universe. I have in mind the simple axiom that an infinite world cannot shrink and disappear with time, nor can its energy be dissipated as a result of continued increase of entropy under the second law of thermodynamics. That law is a statistical law based on the study of dead matter and of energy lost in physico-chemical phenomena of such matter. It is not applicable to living organisms. Since the time when Helmholtz first expressed his doubt of its application to the phenomena of life, several attempts have been made to elucidate this point. Vernadsky emphasized the difference between living and inanimate nature in respect to the second law of thermodynamics. I mentioned it in several articles. Schroedinger in 1945 in his book *What is Life?* says on page 72: "What an organism feeds upon is negative entropy. Or, to put it less paradoxically, the essential thing in metabolism is that the organism succeeds in freeing itself from all the entropy it cannot help producing while alive." It is, I believe, possible to show that Einstein's

celebrated formula $E = mc^2$ asserting that energy is equal to the mass multiplied by the square of the velocity of light, is not applicable to living beings. It does give the measure of energy in a corpse, as it does in a pound of matter where it was successfully used for the production of the atomic bomb. That is all the energy one could derive from a corpse as well as from an equivalent mass of dead matter. But the *living* organism produces work. Even a man-made machine is in that respect different from its equivalent in weight of metal, because of the design incorporated in its construction, which makes it possible to put the machine to useful work. But a living being possesses memory in addition to the ability to work, and consequently is able to learn. The amount of energy dissipated in acquiring knowledge by repeated experience and still more so by a process of creative thought is unquestionably greater than the amount which must be dissipated in learning already available knowledge. The engineer who builds a bridge or an engine, does not have to invent all the methods employed in smelting ore, making tools for the production of saws, hammers, bolts and nails, wheels and cylinders; he does not have to spend his time and energy on developing the principles of mathematics or the methods for determining the stress of materials. He uses his knowledge acquired by learning and thus, beginning at a higher level than his predecessors, avoids the expenditure of energy which potentially would have to be spent over and over again on each occasion if knowledge disappeared from the earth. Viewed in the light of these facts life may be regarded as the means by which nature restores its balance of energy. An exact experimental proof of this function of life would be impossible, but the proof that it is not so, that this interpretation of life is incorrect again would be a burden on the shoulders of those who reject it, for daily experience demonstrates *ad oculos* the conservation of time and energy by learning. Nor is learning restricted to man. It is widely distributed in at least the animal world, and in its lowest form, as conditioned reflexes is used in experiments with even the lowest invertebrates.

It is natural that man should have everywhere unconsciously considered as *good* whatever promotes, guards or aids life, and as *bad* or evil anything that destroys, endangers or incapacitates it. We, with better understanding of the problem and by a more philosophical approach to its solution, based on greater scientific knowledge

and wider experience may consider the balance of energy in the world as its inalienable attribute and call it *good*. Any conscious act toward the conservation of this balance would, under our definition, be good, any conscious act obstructing or nullifying the creative work of life would be evil. The distinction would help us in appraising an act involving a relative value by making it possible to refer it to the absolute standard of balance of energy in the universe as an attribute of infinity. Thus, in general, killing would appear as evil, but when the victim is a criminal whose acts of violence dissipate more energy than his own life conserves, then his execution would be justified. And it would not change an iota in regard to the justice of our verdict if an evil act were committed to enhance the living advantages of a single nation, for that would lower the level of corresponding faculties in other nations. Survival of the fittest could be considered as good only when it is in harmony with a trend toward the realization of the ultimate balance of energy. It would be bad, if it worked against it. In the presence of possible alternatives perceived by a conscious mind, only such a choice of one of the alternatives translated into action can be considered as an act for which the individual is responsible, in contradistinction to acts in which choice was impossible or the mind inoperative. *I choose, therefore I can*; and being able to do so, we are responsible for what we are consciously doing, both as individuals and as nations.

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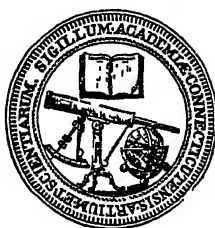
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Problems of Evolution

BY

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Medicine of U.S.S.R.



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BY THE SAME AUTHOR:

THE STRUGGLE FOR EXISTENCE (1934)

VERIFICATIONS EXPERIMENTALES DE LA THEORIE MATHEMATIQUE

DE LA LUTTE POUR LA VIE (1935)

OPTICAL ACTIVITY AND LIVING MATTER (1941)

PREFACE

It is obvious that the study of evolution to-morrow will differ from what it is to-day. New facts will be discovered, and new fields of research will be opened in the domain of biology. Some weak indications of the fields that will probably be the favorites of to-morrow certainly exist even to-day. They lead either a miserable existence as problems which are unduly neglected by modern evolutionists, or are cultivated in some very specialized departments and have thus not had sufficient opportunity to be disseminated.

It is the object of this work to discuss a few relatively neglected problems of evolution, which in the author's opinion may lay claim to be considered the important beginnings of the new trends in biology. We start with the process known as organic selection, the replacement of adaptive modification by adaptive mutations. This idea was born in America about fifty years ago, but is almost entirely forgotten. It was independently and vividly discussed in recent times by a number of Russian biologists. Stimulated by these theoretic discussions I undertook experimental work in this field, and was able to give the first experimental proof of organic selection. But the experimental work permitted us to do more than that; it revealed the existence of an important and hitherto unsuspected principle of inverse relation between phenotypic plasticity and genotypic specialization among different races of the same species. In an attempt at a further generalization of this phenomenon, in which my teacher and friend Prof. W. W. Alpatov took a great part, it was concluded that the phenomenon is due to the compensatory relation between acquired characters and initial properties, which is deeply rooted in the organization of living systems.

It is hoped that an account of these investigations will stimulate further work in this important field.

G. F. GAUSE

Moscow, 1946

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PROBLEMS OF EVOLUTION

I. THE PRINCIPLE OF ORGANIC SELECTION.

1. THE ORIGIN OF THE CONCEPT.

Baldwin (1896, 1902), Osborn (1897) and Lloyd Morgan (1900) suggested about half a century ago that modifications repeated for a number of generations may serve as the first step in evolutionary change, not by becoming impressed upon the germ-plasm, but by holding the strain in an environment where mutations tending in the same direction will be selected and incorporated into the constitution. This process simulates Lamarckism but actually consists in the replacement of adaptive modifications by adaptive mutations.

As Lloyd Morgan wrote in 1900, "any hereditary variations which coincide in direction with modifications of behaviour due to acquired habit would be favoured and fostered; while such variations as occurred on other and divergent lines would tend to be weeded out. Professor Baldwin, who has independently suggested such relation between modification and variation, has applied to the process the term "Organic selection"; but it may also be described as the natural selection of coincident variations. Professor Osborn has also indicated the relationship referred to."

These ideas were not occasional by-products of studies aiming at other goals, but represented in fact a whole movement of biological thought. The concept of organic selection was known to, and discussed by, many leading biologists of that period. This is particularly clear from a book by Baldwin (1902) entitled *Development and Evolution*, which its author considered as a sort of handbook on the theory of evolution which makes general use of organic selection. In appendices there are printed numerous statements on organic selection by various biologists.

This whole line of thought came to a dead end: it was practically forgotten. The reasons for this are not difficult to find. At the time of these writings, about 1900, the situation in biology was not sufficiently clarified for any serious study of the principle of organic selection. The classification of variations into two fundamentally distinct categories—modifications and mutations—did not spread

sufficiently far, and the experimental study of natural selection was scarcely begun. Even to-day, as Julian Huxley (1942) truly remarks, this important principle appears to be unduly neglected by modern evolutionists.

It is remarkable for the history of human thought that the principle of organic selection was independently discovered in Russia about 1936. In that year Dr. Lukin published an important theoretical paper entitled: "On the causes of substitution of modifications by mutations from the viewpoint of the theory of natural selection." In this work the author considered parallelism between phenotypic and genotypic variability, and arrived at the following conclusions: (1) Organisms frequently respond to environmental changes by adaptive phenotypic modifications. (2) Similar adaptive characters may be genotypically fixed in races normally living in the corresponding environments. (3) It is proved that conversion of modifications into mutations is not possible. (4) Hence modifications can only be *substituted* by coincident mutations, if the latter are associated with some advantages in the process of natural selection.

It is clear that Lukin re-discovered the principle of organic selection, which was not known to him and was entirely forgotten at the time of his writing. In a later book: *Darwinism and geographic regularities in variation of organisms* published in Moscow in the Russian language in 1940, Lukin gave a penetrating theoretical analysis of the possible advantages of genotypic adaptation over phenotypic, which might be responsible for the replacement of the latter by the former. Genotypic specialization is preferable to phenotypic plasticity in cases where it is more efficient as, for example, where an early appearance of an adaptive character in the ontogeny is desirable. To take but one example, skin callosities may develop either as a response of the skin to pressure or as a genetically fixed character arising in the embryo, without the stimulus of pressure. The former method exposes the animal to risks during the process of formation of callosities, while the latter protects it from birth onwards.

The process of substitution of modifications by mutations through natural selection was also profitably discussed at about the same time by a number of other Russian biologists. Schmalhausen (1939) in his book *Ways and rules of the evolutionary process* suggested for it the term "stabilizing selection" in as much as the unstable pheno-

typic response of an organism to the change of environment is here replaced by the stable genotypic one. Consequently the response itself becomes "stabilized." Kirpitchenkov (1944) proposed for the same process the term "coincident selection," in as much as modifications are replaced by coincident mutations. The terms organic, stabilizing, and coincident selection are practically synonymous.

It is indeed remarkable that theoretical studies by Lukin, Schmalhausen and Kirpitchenkov reveal so very much in common with those of Baldwin, Lloyd Morgan and Osborn, though they are quite independent. But at the time of the Russian studies biology was already ripe for direct experimental research along these lines. These theoretic studies were therefore more fortunate than their predecessors. They induced a whole line of experimental investigations, some of which will be summarized in the following pages.

2. THE ADAPTIVE VALUE OF MODIFICATIONS.

It is clear that the theory of organic selection is based upon the consideration of adaptive values. It is believed that modifications are adaptive, but it is also implied that their adaptive values are in the long run overpowered by those of genovariations. Any direct investigation of the principle of organic selection should therefore begin with the objective analysis of the adaptive value of different reactions of an organism to the change of environment.

To measure the adaptive value of any specific genovariation is not difficult. It will be sufficient to study the rate of growth of the population in mutants and in normal individuals. The rate of population growth can be used as a criterion of fitness. A mutation slowing down the rate of population growth will possess a negative adaptive value; a mutation enhancing the multiplication over the normal rate will possess positive adaptive value.

To measure the adaptive value of a phenotypic reaction (modification) is much more difficult. In response to the changed conditions all the animals of a given population produce modifications, and no controls which would not bear any specific modification under the changed conditions are left for comparison. It is therefore impossible to say whether any particular modification possesses adaptive value, and what is the magnitude of that value.

For measuring adaptive values of modifications a different method must be used. It is well known that different races of the same

species possess innate differences in adaptability: some of them yield strong modifications, the others weak ones, *under the same change of environment*. In this way, working with different races one gets access to *different dosages* of any specific modification, all other conditions being equal. It is then possible to enquire whether any relation exists between the magnitude of a modification and the rate of multiplication of the organism bearing it. Let us admit that the greater the modification, the better an animal multiplies itself under the new conditions. Such an observation is sufficient to conclude that the modification in question possesses a positive adaptive value. But if the magnitude of a modification is not correlated with the rapidity of multiplication of the organism bearing it, one can safely conclude that such a modification has no adaptive significance.

In order to analyse this problem we have made experiments with 11 different races of the ciliate, *Paramecium bursaria* (Gause, 1941). These races strongly differed from each other in size and form, and were isolated from several small rivers in the environs of Moscow. The infusoria were cultivated in the standard medium containing yeast *Torula utilis*, which is separately grown on solid agar and added in the quantity of 15 loops per 40 cc of the medium. In one series of experiments all 11 races were cultured at 18° C. In the other series the same races were for a month cultivated at 27° C. Finally, in the third series a salt solution (the chlorides of sodium, potassium, calcium and magnesium in the balanced proportion corresponding to sea water) was added to the medium. In the course of a month the salinity was brought to 0.2%, at 18° C. The infusoria were cultivated in small vials and subcultured every five days. All three series of experiments were run in thermostats with glass walls. Finally, the size and division rate of infusoria were measured.

Let us at first consider the following problem: does there exist any relation between the somatic properties of a given race of infusoria (for example, its body surface) and the division rate of the same race? This point is illustrated by Fig. 1. It is evident that in the usual conditions of existence at 18° C there is no regular connection between body surface and division rate. Among smaller as well as among larger races of infusoria there are both slowly and rapidly dividing ones. However, such a picture is profoundly different at 0.2% salinity of the medium. In this case the small races multiply more rapidly than the large ones. The advantage of smaller

rates under increased salinity becomes more clear as one calculates the rate of increase in biomass. Multiplying the body surface (which

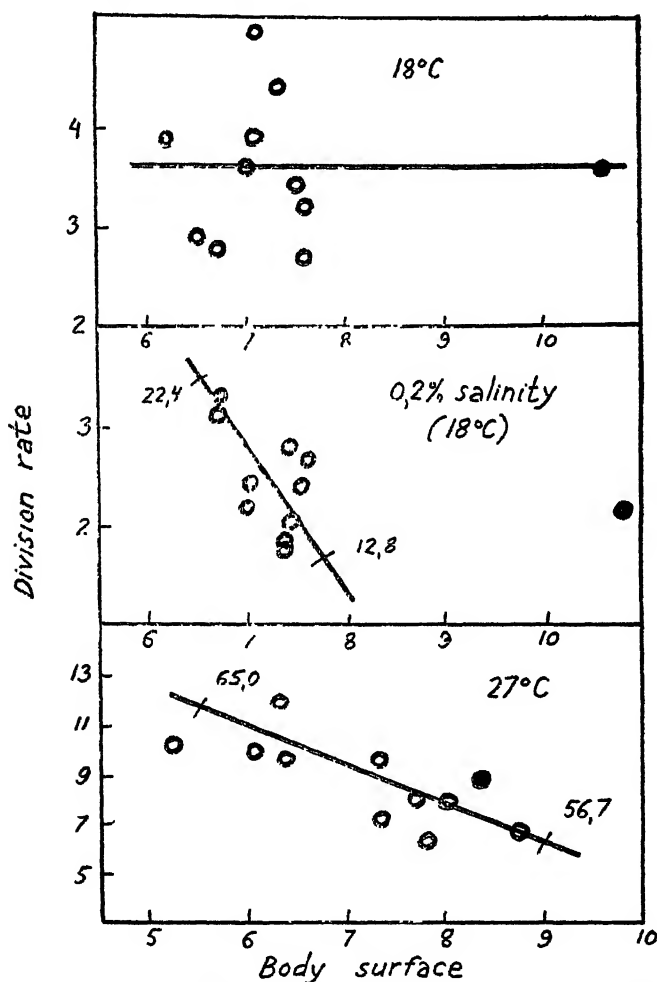


FIG. 1. The relation between the body surface and the division rate in different races of *Parametium bursaria* under various conditions. From Gause (1941b).

is proportional to the biomass) by the rate of division, one can see that the rate of increase in biomass per unit of time in the smaller races attains 22.4, whereas in the larger races it reaches only 12.8. It follows that in the mixed populations growing under increased

salinity, the small races must take hold of the nutritive resources more rapidly than do the larger ones.

A similar picture appears with increased temperature of the medium (27° C). Smaller races again multiply more rapidly than larger ones, and reveal greater coefficients of increase in biomass (65.0 against 56.7). We are led to conclude that the smaller body size possesses adaptive value with increased temperature.

What physiological mechanism lies at the bottom of these facts? Some suggestions in this direction were made by Winberg (1937), who pointed out that with increased temperature the conditions of transport of nutritive substances and of products of metabolism do not increase in the proportions required by the rising needs of cells, owing to a relatively low value of the temperature coefficient of diffusion. Hence at higher temperatures a small body size is an advantage, being associated with better conditions of inflow and outflow of the products of metabolism.

The analysis of experimental data and some theoretical considerations lead us consequently to conclude that in infusoria under increased temperatures and salinities a small body size will possess adaptive significance. In this connection we must expect that every reduction of body size by means of modification should be also useful. It was observed by us that under increased salinity some races of *Paramecium bursaria* decrease in size, some of them do not change in dimensions, while some others even somewhat increase. Correspondingly, one observes in these races this or that change of multiplication in relation to normal rates, as observed under initial conditions of existence. Fig. 2 shows that the more strongly the body surface is decreased by modification, the less the given race slows down its rate of reproduction when cultivated under increased salinity. This experiment can be considered as a proof of the adaptive value of the modification in question, and at the same time serves as a basis for further analysis of organic selection in ciliates.

II. THE EXPERIMENTAL PROOF OF ORGANIC SELECTION.

1. CILIATES AS EXPERIMENTAL MATERIAL.

Various ciliates offer excellent opportunities for experimental studies of organic selection. The genetics of Protozoa is now sufficiently advanced by the work of Jennings and his school, and the

laws of heredity in these small animals are found to agree with those observed elsewhere in the organic world. The following technique was used by Gause and his associates in a number of investigations on organic selection. Two vegetatively reproducing clones of the same species of ciliates belonging to opposite mating types were separately placed in the changed environment, and the phenotypic response of each clone in the separate culture was observed. At the same time a mixed culture of these two opposite mating types was

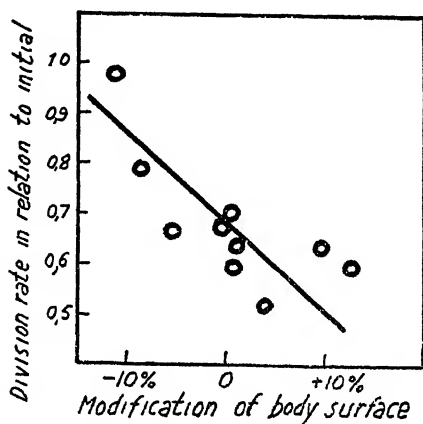


FIG. 2. The relation between the modification of body surface and the decrease in the rate of division in different races of *Paramecium bursaria* transferred from fresh water (synthetic medium of Beers) to 0.2% of salinity. From Gause (1941b).

placed in the same changed environment. Conjugation took place, giving rise to diversities of various kinds due to re-combination of hereditary material. Those hereditary variations that were occasionally more fit, survived and supplanted their competitors after a number of generations. After some time it was possible to compare phenotypic responses to the changed environment, as observed in the separate cultures, with the naturally selected best genotypic response in the mixed culture. Are modifications really replaced by coincident mutations? What, if any, are the advantages of the genotypic response over the phenotypic one? To what extent do phenotypes of the coincident mutations really coincide with the modifications which they substitute? These and similar questions can be answered by direct experiments.

2. THE ROLE OF ORGANIC SELECTION IN THE ACCLIMATIZATION OF EUPLOTES TO DIFFERENT SALINITIES.

Invertebrates inhabiting saline waters have repeatedly been the object of investigation as regards adaptive processes. Two papers published by Gause (1940a, 1941a) deal with the acclimatization of the ciliate *Euplotes vannus* to different salinities. This infusorian was collected in a salt lake near Odessa, with a salinity of 2.5 per cent at the time of collection. For technical details of this work the original article should be consulted (Gause, 1941a).

Euplotes vannus, cultivated in the laboratory at 2.5 per cent of salinity, easily withstands a sudden transfer to 5 per cent salinity. This tolerance is probably due to the fact that the salinity of the lake from which it comes sometimes attains about 5 per cent in the dry period. When infusoria are cultivated for some time at 5 per cent salinity in pure clones in the laboratory, the body size of all clones distinctly diminishes as compared to that observed in the 2.5 per cent medium. For example, in clone 7a the surface of the body decreases by 2.2 per cent, in 7b by 9.9 per cent, in 10a by 20.1 per cent and in 10b by 12.5 per cent. These changes are evidently adaptive, bringing *E. vannus* closer to a smaller species inhabiting more saline waters.

How will the acclimatization of *E. vannus* to 5 per cent salinity be affected by the natural selection of chance inherent variations arising at the time of conjugation of the opposite mating types in the mixed cultures? To elucidate this problem mass conjugation of infusoria was induced by mixing the clones 7a with 7b, and again 10a with 10b, in 2.5 per cent salinity. One hundred conjugating pairs of each combination were directly transferred to 5 per cent salinity, and this experiment was made simultaneously with the beginning of acclimatization of separate clones. Ten days after the beginning of this experiment, another spontaneous mass conjugation occurred in the mixed cultures of infusoria at 5 per cent salinity. The cultures were re-seeded from time to time, and natural selection of the better fit clones, which casually arose at the time of conjugations and appeared to be better adapted for living under increased salinity of the water, took place.

On the twentieth day after the beginning of the experiment, at the time of measurement of individuals living in pure clones, we

also measured those infusoria from the mixed cultures 7ab and 10ab which had survived at 5 per cent salinity. Since the average body surface in clone 7a living separately in the 5 per cent medium attained 96.5 and in clone 7b correspondingly 132.0, it is clear that in the absence of any natural selection the average body surface of individuals from the mixed population 7ab living at 5 per cent salinity should approximately equal the average body surface of the two ancestor lines, i.e., 114.2.

This expectation is supported by studies of inheritance of size at conjugation under controlled conditions in *Euplotes vannus*, reported in detail by Gause (1941a). When the two parental clones differ in their size, the exconjugant clones will be also different, some of them large, the others small. But it was observed that the average size of a great number of offspring clones grown in pure cultures is equal to the mean of the two parental clones.

Returning now to our experiment with the acclimatization of *Euplotes vannus* to the increased salinity of 5 per cent in the mixed culture of exconjugant clones, the average body surface in mixed population attained 107.0, and was considerably less than the average of the ancestor lines (i.e. 114.2) living under the same conditions of increased salinity. In other words, natural selection in a mixed population works in the direction of strengthening the adaptive modification. Under the influence of increased salinity all infusoria in pure clones diminish in size (adaptive modification); at the same time in mixed population relatively smaller clones are selected. It appears that we are dealing here with a case of organic selection, which improves the adaptive modification by selection of casual inherent variations in the same direction.

The same result was obtained with another pair of investigated clones. The average body surface in the clone 10a living separately at 5 per cent salinity is 81.5, in the clone 10b correspondingly 79.9. The average body surface of the mixed culture living in a medium of 5 per cent salinity in the absence of natural selection should be equal to 80.7. The average actual body surface in the progeny of conjugants 10ab, living at 5 per cent salinity, was 74.9. Here is again evident the operation of organic selection, intensifying the adaptive decrease of size by the way of natural selection of smaller clones in the mixed culture.

Fig. 3 represents graphically the effect of organic selection in the

acclimatization of clones 7a and b of *Euplotes vannus* to 5 per cent salinity.

Let us now turn to the acclimatization of *Euplotes vannus* to the increased salinity of 7 per cent. If, starting from the initial 2.5 per cent, the salinity in the cultures of pure clones of *E. vannus* is increased and in a month brought to 7 per cent, the infusoria begin to degenerate and soon perish. These results were obtained not only with the four clones already mentioned (7a, 7b, 10a, 10b),

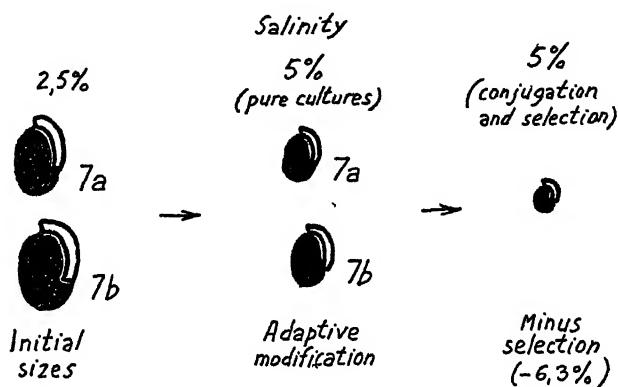


FIG. 3. A schematic representation of organic selection in cultures of *Euplotes vannus* at 5 per cent salinity.

but also with six other strains (2b, 4a, 5a, 5b, 8a, 8b). A gradual degeneration and disappearance of infusoria is also observed in consequence of the direct transfer of individuals from various clones from 2.5 salinity to 7 per cent. After the fifteenth to seventeenth days of cultivation they steadily disappear. It is clear that these infusoria are unable to produce any adaptive somatic modification under such a profound alteration of conditions as the increase of salinity up to 7 per cent.

But when 200-300 conjugating pairs, or 500-600 early exconjugants, are directly transferred from a 2.5 to a 7 per cent medium, in one-half of the experiments *E. vannus* develops satisfactorily, and on the fifteenth to seventeenth days of the experiment the culture is moderately flourishing. It is clear that in the process of recombination of hereditary material at the time of conjugation new strains are produced, and some of these appear to be adapted to such extreme conditions of existence as 7 per cent salinity. This

experiment was repeated twelve times. It can be taken as an example of adaptation of an organism to extreme conditions of existence, where adaptive somatic modification is not any longer possible. In this case direct natural selection takes the place of casual inherent favorable variations arising at the time of conjugation.

It could perhaps be objected that the survival of exconjugants and the disappearance of non-conjugants in 7 per cent solutions is not due to genetic recombination of characters, but rather to a difference between the "young" or "rejuvenated" exconjugants and the less vigorous original clones. This explanation is not admissible for the following reason. It is not all exconjugants, but only a very small fraction of them that can survive in 7 per cent solutions. When 600 exconjugants were placed in each experimental vessel the survival of infusoria was recorded only in 50 per cent of experiments. It follows that the resistant clones appear with the approximate frequency of one per 1200 of exconjugants. Such a frequency strongly suggests that it is a genetic, and not a physiological consequence of conjugation that is of importance for the acclimatization of *E. vannus* to the increased salinity of 7 per cent.

We have further attempted to acclimatize *Euplotes vannus* to the decreased salinity of 1 per cent. It was found that the clones studied were mostly unable to form adaptive somatic modifications to such a considerable decrease of the salinity of the medium; they are unable to gain in body size. The absence of the capability of adaptive somatic gain in body size in decreased salinities can be correlated with the probable previous history of the species *Euplotes vannus*. It evidently entered saline waters directly from the sea, and never before lived in fresh waters. Here is the apparent reason for absence in this species of adaptive modifications in the fresh-water direction.

What will be the effect of natural selection in conditions of 1 per cent salinity? To elucidate this point, 100-200 conjugating pairs (7ab or 10ab) were transferred from 2.5 per cent directly into 1 per cent medium. The viable exconjugants were subject to natural selection, and on the twentieth day after the beginning of the experiment the usual measurements were made.

The calculation of the surface of the body shows that in the pure clone 10a at 1 per cent salinity the body surface attains 101.5 and in the clone 10b correspondingly 119.5. The average body surface in

the population 10ab in the absence of natural selection should be 110.5. The actual body surface observed in the same population is 115.6. The excess over the average body surface is + 4.6 per cent. It is clear that natural selection here favours larger individuals.

The corresponding data for the population 7ab are as follows. The body surface in the clone 7a at 1 per cent salinity is 98.0, in the clone 7b correspondingly 136.7. The average body surface in the absence of natural selection should be 117.3. The actually observed surface of the body in the progeny of exconjugants 7ab is 139.0. The excess over the average body surface is + 18.6 per cent.

We are consequently led to conclude that with the decrease of salinity to 1 per cent, *E. vannus* is not subject to the adaptive physiological gain in size, but in spite of this in mixed culture there takes place direct natural selection of inherently larger clones, which are better fit for the specific conditions of living in decreased salinities.

Summing now up the results of these studies it can be stated that with increase in salinity of the medium from 2.5 to 5 per cent the body size in various clones of *E. vannus* diminishes. Conjugation in mixed cultures of two opposite mating types and subsequent natural selection at 5 per cent salinity favours the survival of relatively smaller strains. Natural selection works here in the same direction as adaptive modification, and this case could consequently be considered as an example of organic selection.

With increase of salinity of the medium to 7 per cent, adaptive modifications in *E. vannus* are no longer formed and various strains entirely die out. Among exconjugants direct natural selection of viable individuals occurs. If such variants occasionally appear, they become ancestors of the culture that continues living. In this case there is clearly no organic selection.

With decrease of salinity of the medium to 1 per cent, the adaptive increase of the body size in various clones of *E. vannus* does not take place. The adaptive somatic modification is probably impossible in this case because *E. vannus* never inhabited fresh water in its past history. Among exconjugants direct natural selection of individuals of larger body size occurs. In this case, too, organic selection is not found.

It is clear from all this evidence that the possibilities of genotypic response to changed environment are much wider than phenotypic ones. Hence with extreme alteration of conditions direct natural

selection of genoadaptations takes place, but when the environment changes less drastically the work of organic selection can be observed with certainty. So far as is known this is the first case of the experimental demonstration of organic selection.

3. THE ROLE OF ORGANIC SELECTION IN THE ADAPTATION OF PARAMECIUM TO DIFFERENT TEMPERATURES.

Investigations published by Smaragdova (1941) and by Gause, Smaragdova and Alpatov (1942) proved the existence of geographical variation in various species of the genus *Paramecium*. It was observed that the temperature optimum for the division rate is different in *Paramecia* of different geographical origin. Significant differences were recorded between Moscow and Southern clones of *Paramecium aureliu*, and between Moscow, Northern and Southern clones of *Paramecium bursaria*. Generally speaking, optimal temperature for multiplication of *Paramecia* increases from north to south and closely depends upon the average summer temperature of the locality of origin. For example, temperature optimum for multiplication of *Paramecium bursaria* is as follows: northern clones (collected in the region of the White Sea) $23.96^{\circ} \text{C} \pm 0.30$, Moscow clones $28.41^{\circ} \text{C} \pm 0.18$; southern clones (Odessa) $28.94^{\circ} \text{C} \pm 0.14$. These differences are hereditary and are maintained when animals are cultivated for hundreds of generations under uniform laboratory conditions. A similar picture was observed by Mishustin (1939) with soil bacteria (*Bacillus mycoides*).

More detailed studies of geographic variation were made by us on body size of *Paramecium bursaria*. It was found that body size in this species regularly decreases from north to south. These differences are hereditary, but recall somatic non-hereditary temperature modifications. It was further recorded that in crossing different geographical forms of *Paramecium bursaria* the greatest mortality of exconjugants is found when Northern clones are crossed with Moscow or with Southern ones, and the lowest mortality when Moscow clones are crossed with each other. The rise of non-viability in hybrids of remote geographical forms is probably associated with the increase of chromosomalgenic incongruity of their genomes. A documented record of these observations was published by Gause, Smaragdova and Alpatov (1942). More recently, Jennings and Opitz (1944)

reported that crosses between Russian and American varieties of *Paramecium bursaria* are lethal to both of them.

The study of geographical variation in *Paramecium bursaria* shortly outlined above has led us to conclude that in warmer climate the body size of this species is diminished and genotypically fixed. At the same time it recalls somatic phenotypic temperature modifications. Is organic selection responsible for the origin of geographical diversities by the substitution of phenoadaptations by genoadaptations?

In order to approach this problem a detailed study was made of the effect of organic selection in the adaptation of *Paramecium bursaria* to different temperature conditions. The technique of this work was similar to that used in the work with *Euplotes*, and its results were published partly by Gause, Smaragdova and Alpatov (1942) and partly by Gause (1941b). Conjugating pairs of two Moscow clones of *P. bursaria* (1A and 2A) belonging to opposite mating types were placed at two temperatures, 13.4°C and 25.4°C, 50 pairs in each of two vessels. For controls pure clones 1A and 2A were used at the same temperatures and densities. *Paramecia* were bred in these conditions for two months, with frequent re-inoculations into fresh medium, and were then measured.

If in mixed cultures there were no natural selection among progeny of exconjugants, the average body surface of individuals from such cultures should be equal to the average surface of the two ancestral clones. Experiments showed, however, that at low temperature the surviving progeny of exconjugants is by 11.5% larger and at high temperature 7.6% smaller, than the average of ancestral clones living under the same temperature conditions and yielding usual temperature modifications. Hence it is reasonable to conclude that the new biotypes casually arising at the time of recombination of hereditary material in the sexual process are of importance for natural selection. At lower temperatures the advantage belongs to the larger forms, whereas at higher temperatures the smaller biotypes are advantageous. These relations are presented graphically in Fig. 4.

This experimental proof of organic selection was further supplemented by additional control cultures. No attention was heretofore paid to the inheritance of body-size at conjugation in *Paramecium bursaria*, and it was assumed that in the absence of natural selection

the average body surface of the progeny of exconjugants must coincide with the average body surface of both parental clones. In order to get an insight into this phenomenon we crossed two Moscow clones of opposite mating types, 6 and 2B, at 18° C, and then placed at the increased temperature of 27° C *firstly*, the parental

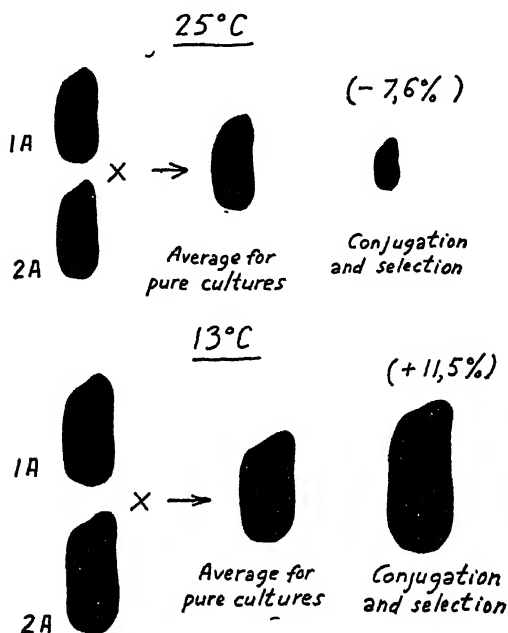


FIG. 4. A schematic representation of organic selection in cultures of *Paramecium bursaria* at different temperatures.

clones in three parallel pure cultures; *secondly*, twenty-five exconjugant clones taken at random, each of them in pure culture; *thirdly*, seven mixed cultures, each of which consisted of all twenty-five exconjugant clones. The cultivation at 27° C was conducted in small vials for one month, with five re-inoculations of all cultures. Afterwards the infusoria were measured. The results of these measurements are presented in Table 1.

Although exconjugants in pure lines differed in their body-size from one culture to another, their average body surface (6.64) turned out to be pretty close to the average parental values (7.03).

As far as the mixed population of exconjugants is concerned, we

can record a very distinct and entirely significant decrease in dimensions in comparison to the average parental values. The average body surface in mixed cultures attains 5.74. In this way organic selection manifests itself sufficiently clearly.

TABLE 1
Body size of *Paramecium bursaria* in different cultures at 27° C.
From Gause (1941b).

Culture	Number of measurements	Length of the body ($1 = 16.7\mu$)	Width of the body	Body surface
Parental No. 6	60	8.42 ± 0.053	4.17 ± 0.039	8.76
Parental 2B	60	7.42 ± 0.041	2.86 ± 0.026	5.30
Average of parents	7.92 ± 0.067	3.51 ± 0.047	7.03
Exconjugants in pure cultures	500	7.86 ± 0.020	3.38 ± 0.015	6.64
Exconjugants in mixed culture	140	7.56 ± 0.033	3.04 ± 0.023	5.74

We have every reason to suspect that the similarity between the results brought about by organic selection and by the temperature modifications consists only in a superficial likeness. For example, in the populations of *Paramecium bursaria* at 27° C there takes place not only a decrease in body-size, but also a change in bodily proportions in relation to the average parental values. The ratio length: width attained in the clone No. 6 2.02, in the clone 2B 2.59, the average of these two figures being 2.305; in the pure cultures of exconjugants on the average 2.33, and in the mixed cultures 2.49. It is clear that the change of proportions in individuals from mixed culture represents a result of preferential distribution in the mixed population of smaller but at the same time more narrow ancestral type of the clone 2B. In this way a selection for small body-size, owing to the occasional genotypic constitution of a population, turns out to be a selection for narrow body form. There are evidently no reasons for such a particular correlation of these two characters in the case of a temperature modification.

Summing up the results of these studies it can be concluded that organic selection plays an important part in the adaptation of *Paramecium bursaria* to different temperature conditions. At increased temperatures the body size in all clones decreases by phenotypic modification, and at the same time an intensive selection of inherent

variations decreasing the body size goes on inasmuch as smaller body size is associated with increased fitness. It is probable that organic selection has played an important part in the geographical differentiation of this species.

4. THE RESEMBLANCE OF GENETIC ADAPTATIONS TO ADAPTIVE MODIFICATIONS.

It is unlikely on *a priori* grounds that the resemblance of genoadaptations to phenoadaptations which they substitute will be a far-reaching one. As far as substituting or organic selection is based upon a greater adaptive value of possible genovariations as compared to modifications, and not upon the inheritance of the latter, it is probable that the likeness between these two types of acquirement will be limited to a superficial resemblance only. It is hardly reasonable to expect that genoadaptation will imitate all particulars of a physiological response.

However, this important problem represents an attractive field for further investigations. It would be useful to undertake some detailed comparisons of inherent geographic diversities, which originated in the long process of historic development, with corresponding modifications. Such comparisons can be better made in insects than in Protozoa, since the chitinous skeleton of the former is particularly appropriate for various accurate measurements.

With the purpose of initiating an investigation in this direction we studied geographic variation in the small housefly, *Fannia canicularis* L. A part of the material was collected in the Crimea in the environs of the Karadag Biological Station on May 23–26. Some of the insects collected were immediately fixed in 80% alcohol. Besides, a number of fertilized females was distributed among bottles with the nutritive medium (moist bran and a few drops of ammonium chloride solution). Afterwards, the same species was collected in Moscow on June 6–8. Again, some flies were fixed, while a number of fertilized females were kept for multiplication.

All experiments were made in the Moscow laboratory. At the beginning of an experiment, the newly hatched larvae were distributed among the bottles with fresh nutritive medium, 20 individuals being placed in each bottle. Both Moscow and Crimean flies were kept in the thermostat at 21.6° C. In order to obtain

temperature modifications, each Moscow line was kept in two parallel bottles, one of which was put into 21.6° C while the other was kept at 28.5° C.

The flies, which began to hatch towards the end of June, were fixed by 80% alcohol. Their dextral wings and right middle legs were mounted in glycerine under cover glasses, while the body was boiled in KOH solution, the fourth tergite separated and also mounted under the cover glass.

The measurements of characters were made under the microscope with the aid of an ocular-micrometer. The average values of characters measured and their probable errors were published by Gause (1941b) and need not be repeated here.

A comparison of Moscow and Crimean flies collected in nature at the same time in the spring shows that the southern flies are smaller. In females this difference is more distinct and entirely significant. In this way *Fannia* reveals geographic variation in agreement with Bergmann's rule (the increase of dimensions to the north).

It is certainly impossible to conclude whether these differences recorded under natural conditions are phenotypic or inherent. However, a further comparison of southern and Moscow flies reared in the laboratory under identical environmental conditions shows that the strong and significant differences between them are retained. In this way southern flies appear to be inherently smaller than the northern ones.

Under the action of increased temperature Moscow flies show reduction in dimensions and become even smaller than are the Southern ones. In this way, *Fannia canicularis* reveals a picture very close to that observed in *Paramecium bursaria*. In both these animals there is a general somatic similarity between non-hereditary temperature modifications and inherent geographic diversities.

In the case of *Fannia canicularis*, the degree of resemblance between modifications and inherent geographic diversities can be subjected to a more detailed analysis. For that purpose we calculated bodily proportions observed in the case of temperature modifications and of inherent geographic diversities, and have presented the results represented in Table 2.

This table shows that with the decrease of body size by means of modification and by means of inherent geographic alteration, the

TABLE 2

The bodily proportions in the case of modifications and of inherent geographic diversities in the small housefly, *Fannia canicularis* L. From Gause (1941b).

Indices	Males			Females		
	Moscow 21.6°	Crim 2 21.6°	Moscow 28.5°	Moscow 21.6°	Crimea 21.6°	Moscow 28.5°
1. Length of the wing: Tergum	5.37	5.48	5.59	5.06	5.28	4.87
2. Width of the wing: Tergum	2.96	3.03	3.08	2.81	2.92	2.70
3. Femur: Tergum	2.36	2.34	2.43	2.11	2.18	2.09
4. Tibia: Tergum	2.24	2.24	2.33	2.03	2.09	2.03
5 Length of the wing: Width of the wing	1.81	1.81	1.82	1.80	1.81	1.80

proportions between different organs change in two different manners. The southern males are characterized by greater relative length of wings as compared to Moscow males, and at the same time by an identical relative length of legs. However, in the case of temperature modification of the Moscow males they increase the relative length of both wings and legs. In this way one detects the difference in the mechanism of the adaptive adjustment of an organism by means of modification and of genoadaptation; in spite of the general somatic resemblance detailed coincidence between these two kinds of change is lacking.

A similar picture is observed in females. The southern flies are characterized by much greater relative length of wings and only slightly increased relative length of legs. In contrast to this, the temperature modification of Moscow female flies brings about a slight decrease in the relative length of wings, with the approximate constancy of legs. There is certainly an urgent need for further studies in this important field.

III. THE RELATION OF PHENOTYPIC PLASTICITY TO GENOTYPIC SPECIALIZATION.

1. THE INVERSE RELATION BETWEEN ACQUIRED AND INHERENT RESISTANCE.

The relation between plasticity and specialization of organic forms represents a favorite subject for speculations and research in the field of palaeontology, and it is curious that this important problem has

escaped any adequate treatment in the field of micro-evolution. Is there any regular relation of phenotypic plasticity to genotypic specialization among different races belonging to the same species?

To investigate this point, we have recently undertaken some studies on unicellular animals (Gause and Smaragdova, 1939; Gause, 1940b; Smaragdova, 1940). Let us now summarize briefly some of the results obtained.

Gause and Smaragdova (1939) studied the adaptation of fresh-water infusoria (*Paramecium caudatum*, *P. aurelia* and *P. bursaria*) to increased salinity of the medium. In order to get access to a wide range of hereditary variability, the sexual process (conjugation) was induced in each species. According to the older data of Jennings (1913), confirmed more recently by Raffel (1930), and also by Jennings, Raffel, Lynch and Sonneborn (1932), recombination of hereditary material at the time of conjugation produces numerous inherent variations in morphological and physiological characteristics of *Paramecium*, so that after conjugation a great number of clones can be isolated which will differ strongly in all their properties.

Gause and Smaragdova studied the adaptation of a considerable number of exconjugant clones in each species of infusoria to gradually increasing salinity of the medium. At the start, the initial resistance to salinity, before the beginning of the process of adaptation, was recorded for each clone, and later the increased resistance to salinity at different stages of the adaptive process. The difference between the subsequent and the initial resistance yielded the value of modification.¹ The resistance to salinity was measured by the concentration of salts killing 50% of the individuals in one day. For the purpose of these measurements the infusoria were at first equalized in respect to the nutritive conditions. Fifty individuals of each line were placed for a day in 5 cc of the nutritive medium (salt solution containing a suspension of *Bacillus subtilis* and *Torula utilis* previously grown on agar media). Infusoria were then taken from such a preparatory culture and placed by groups of four individuals into each depression slide. To each group were added 8 drops of standard saline medium in this or that concentration (0.3%, 0.4%, 0.5% etc.) without food. The cultures were left at 25° C and on

¹ Modification in this case is the increased resistance due to a direct effect of environment upon the organism of *Paramecium*. At the bottom of this process lie the alterations of intracellular structures.

the following day the number of individuals was counted. Experiments with each clone were repeated twice and yielded a curve relating the number of surviving individuals with the salinity of the water. In experiments with *P. caudatum* 245 such curves were obtained. The resistance to salinity in each clone was measured by the concentration of salts killing 50% of individuals per day (i.e. leaving still

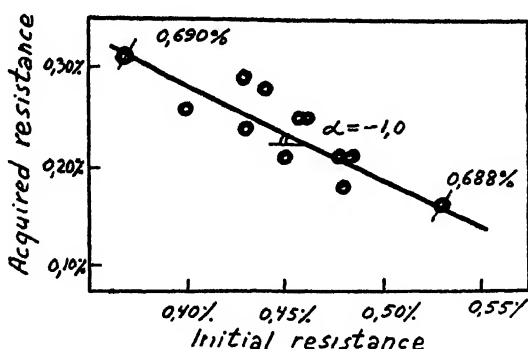


FIG. 5. The relation between the initial resistance to salinity and the acquired resistance in different clones of *Paramecium caudatum*. From Gause (1940b).

alive 2 individuals out of 4). This value was read from the concentration-toxicity curve. Experiments with various clones were performed under perfectly identical environmental conditions, and hence differences between clones in the values of both the initial resistance and the modification were due to inherent, genotypic causes.

When the salinity of the medium is increased slowly and later ceases to increase, so that physiological organization of the *Paramecia* approaches a kind of steady state, one comes across a peculiar phenomenon which can be called *complete compensation between genoadaptation and modification*. This regularity is represented on Fig. 5. On the abscissae are plotted values of the inherent adaptation, in this case of the initial resistance to salinity in various clones of *Paramecium caudatum*. On the ordinates are plotted the values of modifications acquired by the same clones. It is clear that the acquired resistance is inversely proportionate to the inherent one: [Acquired resistance] = $b - a$ [Inherent resistance]. The coefficient of inverse proportionality (α) in this case is equal to unity. We are right in concluding that a deficiency in the inherent resistance

(genoadaptation) is entirely compensated by the acquired resistance (modification), in such a way that the sum total of these two characters remains approximately constant within the species *Paramecium caudatum* (0.688%, 0.690%).

It is hence possible to conclude that a casual genotypic increase or weakening of initial adaptation is by no means simply added to the value of the modification. It is instead observed that clones of *Paramecia*, which are genotypically weak at the start, compensate this weakness by the increased capability for formation of modifications. At the same time those clones of *Paramecia*, which are genotypically strong in the initial resistance, possess but weak adaptability.

From a physiological point of view, the strong negative relation between the initial, inherent adaptation and the amount of modification shows that these two characters are not independent but are instead due to activity of one and the same physiological system capable of yielding only a certain fixed amount of total adaptation.

The conclusion just reached concerning the constancy of the total value of adaptation in different clones of infusoria must be viewed in a proper perspective. When the salinity of the medium had for some time ceased to increase, and the process of adaptation of the physiological organization of *Paramecia* approached a kind of steady state, it is true that the total salt-resistance in diverse clones of infusoria is approximately constant, as it is shown in Fig. 5. Experiments show, however, that in the course of active adaptation of *Paramecia* to the increasing salinity of the medium, a characteristic deviation is observed from the constancy of the total resistance.

If in the work with *Paramecium caudatum* the salinity of the medium is gradually increased for a month up to 0.36%, and then maintained at this level for 20 days more, the subsequent test will yield approximate constancy of resistance in diverse clones. If, however, the course of adaptation is more rapid, so that the resistance of the *Paramecia* is measured on the 30th day after the beginning of the experiment when they are brought to 0.36% of salinity, and on the 60th day at 0.60% of salinity, one observes the relation represented in Fig. 6. The relation of initial resistance to salinity of a given clone of *Paramecia* to the amount of modification acquired by it is again negative. However, the sum total of these two characters (i.e. the total adaptation) is no longer even approximately constant in various clones. The gradual increase of the total resist-

ance from right to the left clones in Fig. 6 (0.52; 0.55; 0.57; again 0.85; 0.90; 0.98) is rather peculiar. In other words, clones which are initially weak in resistance acquire such powerful modifications that their total resistance to salinity outruns that of inherently stronger strains. This means that inherently weaker strains are "over-strengthened" by means of modification.

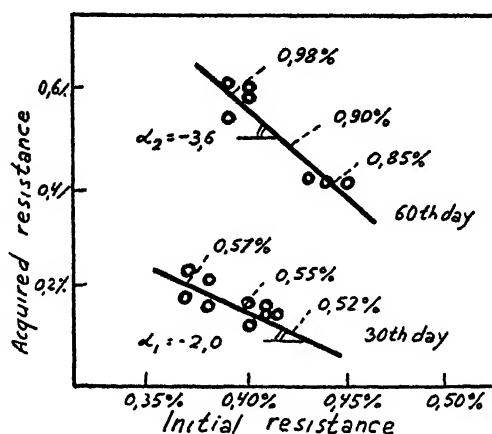


FIG. 6. The relation between the initial resistance to salinity and the acquired resistance in different clones of *Paramecium caudatum* on 30th and 60th days of adaptation to rapidly rising salinity. From Gause (1940b).

Such a characteristic behaviour is best expressed by the value of the coefficient α , which in this case is no longer equal to unity, but equals on the first stage of adaptation 2.0, and later, 3.6. In other words, we are dealing here with the incomplete inverse proportionality between the inherent and acquired properties of organism, which means the incomplete compensation between genoadaptations and modifications.

An inverse relation between the initial resistance to salinity and the magnitude of acquired modification was also observed in experiments with another species, *Paramecium bursaria* (Smaragdova, 1940). Various exconjugant strains of this species were gradually acclimatized in pure cultures to 0.21% of salinity (through the intermediary stages of 0.007%; 0.07%; 0.14%). Their resistance was tested 45 days after the beginning of the experiment, and the results obtained are given in Table 3.

It is clear that the clones 1a₁, 1b₁, S and R possess lower initial

TABLE 3

Resistance to salinity in various clones of *P. bursaria* before and after acclimatization to 0.21% of salinity. Resistance is expressed by the concentration of salt killing 50% of individuals per 24 hours. Each figure is the average data of two series of tests with four experiments in each series.

Number of the clone	Resistance before acclimatization	Resistance after acclimatization	Modification
1a ₁	0.267	0.400	+ 0.133
1b ₁	0.266	0.400	+ 0.134
2a ₁	0.293	0.380	+ 0.087
2b ₁	0.278	0.337	+ 0.059
S	0.264	0.405	+ 0.141
R	0.262	0.400	+ 0.138

resistance as compared to 2a₁ and 2b₁, but at the same time they exceed these latter clones in respect of capability for modification. Adaptability in the inherently weaker clones is so strong, that in respect of total resistance to salinity after acclimatization (i.e. by the total adaptation) these clones overtake initially stronger strains. In other words, in this case an overcompensation of the weak genoadaptations is again evident.

An inverse relation between the inherent and acquired resistance to arsenic in various clones of infusoria, *Colpoda steini*, clearly manifests itself in the data published by Schuckman (1940) and is demonstrated by us in Table 4, although the author himself did not notice this regularity.

TABLE 4

The resistance of *Colpoda steini* to arsenic solution, expressed in maximal tolerant concentration (n/10 As₂O₃ is taken for 100%).
After Schuckman (1940).

Number of the clone	Resistance before adaptation	Resistance after adaptation	Modification
ST I	7%	35%	+ 28%
Mg	13%	30%	+ 17%

It is to be noted that the weak clone ST I here again overcompensates its weakness. Orlova (1940) also observed an inverse relation between the inherent and acquired resistance to calcium chloride in different races of *Paramecium caudatum*.

2. ADAPTATION TO CHANGING ENVIRONMENT.

Returning to the problem of evolution we must draw some conclusions from the observations heretofore reported. It was recorded in the previous chapter, that the possibilities of a genotypic response to the change of environment are much wider than those of a phenotypic response. We are now led to conclude that phenotypic response itself depends upon the amount of genoadaptation already attained. It appears that this conclusion has some important consequences for the adaptation of an organism to changing environment.

The problem of adaptation to *variable* environment is one of the most important problems in the whole study of evolution. Huxley (1940) has well stated it in the following lines: "The giant reptiles of the Mesozoic included the largest carnivores the world has ever seen, like the Tyrannosaurs, and the most heavily armoured animals, like the Stegosaur and the Ceratopsians. They answered bulk with bulk, aggressive with defensive warfare. But they were all doomed to extinction as soon as the *changing environment* gave the insignificant but brainier little mammals their chance."

The conception brought forward by Huxley belongs in the main to Cope (1896) and to other outstanding paleontologists of the last century. These investigators suggested an inverse relation between the specialization and plasticity of organic forms. The greater the specialization, the less the plasticity. When the environment is variable and there is a need for plasticity, the specialized giant reptiles must perish, and the unspecialized but adaptable small mammals acquire a wide distribution.

It is highly remarkable that the generalization of paleontologists based upon the known facts of macro-evolution is entirely substantiated by the experimental investigation of micro-evolution which was just reported. By comparing different races of the same species we observe an inverse relation between the inherent and acquired properties, which is just another term for the same specialization and plasticity.

In what way will the adaptation of an animal to the changing conditions of existence take place? The theory of organic selection points to a substitution of phenoadaptations by genoadaptations only under a relatively constant environment. In the case of a variable environment we can rather expect a further increase of the mag-

nitude of the useful phenoadaptations. It is clear that this problem should be subjected to an experimental analysis.

Gause (1939, 1940), Gause and Smaragdova (1939), and Smaragdova (1940) studied the adaptation of *Paramecia* to rising concentrations of mineral salts and of quinine. The results obtained in the work with *Paramecium caudatum* already have been discussed in the previous section, and presented there in Figures 5 and 6. Which clones of *Paramecium* will survive natural selection in the process of adaptation to rising salinity? It is true that natural selection requires special analysis, and this was already reported at length by Gause (1942) and need not be repeated here. At present let us only discuss briefly the advantages and disadvantages possessed by the various clones. One is inclined to admit that in the adaptation to increasing salinity of the medium the leading part is played by the total resistance to salinity, or in other terms, by the total value of adaptation. Which part of this total resistance is inherent and which is acquired is probably unimportant. It is further apparent that natural selection in the mixed cultures of *Paramecium* will operate throughout the adaptive process. The natural selection of stronger strains certainly will not wait the attainment of the steady state when the adaptation is in the main completed and the various clones are approximately equalized in their properties, as it was shown in Fig. 5. In the course of adaptation to the increasing salinity the total resistance will not be the same in infusoria of various clones. The strongest total resistance will occur in those clones which are weak at the start but powerfully adaptable (Fig. 6). All other conditions being equal, it is these strains which will survive the natural selection.

Natural selection for great total adaptation in the gradually rising salinity will consequently lead to the survival of strains with genotypically weakened initial adaptation and genotypically enhanced adaptive modification. In other words, the natural selection under the conditions of a variable environment will favor the decrease of specialization at the expense of increased plasticity.

The conclusion just arrived at means simply that the mechanism of adaptation of *Paramecium caudatum* to increasing salinity of the medium consists in selection for adaptability. Such a situation is only possible because adaptive modification here constitutes the lion's share of the value of total adaptation. The part played by the value of initial resistance to salinity is relatively small. With a

given total resistance a combination of strong adaptive modification with slight initial resistance appears to be more advantageous than a combination of weak adaptive modification with strong initial resistance. At the same time such combinations as strong adaptability and genotypically strong initial adaptation appear to be impossible for physiological reasons.

Fig. 7 shows graphically the resistance to salinity in various strains of *Paramecium caudatum* before and after rapid acclimatization to

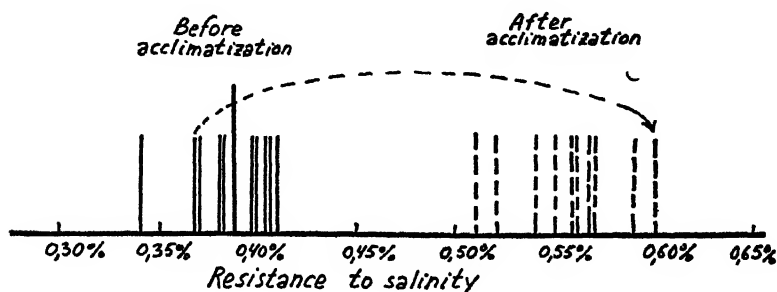


FIG. 7. Resistance to salinity in various clones of *Paramecium caudatum* before and after acclimatization of them to the salinity of 0.36%. From Gause (1940b).

the salinity of 0.36%. The test was made on the 30th day after the beginning of the experiment. One is impressed by the fact that the inherent diversities in the initial resistance to salinity are relatively weak, and they are much overlapped by the capability to form adaptive modifications, which is peculiar to all the strains, and hence by inherent diversities in the adaptability which here arises. The same picture was observed in experiments with 20 diverse strains of the other species, *Paramecium aurelia* (Gause, 1939).

The story heretofore reported shows that a powerful capacity for the formation of adaptive modification is a necessary prerequisite condition for natural selection for adaptability. But the very feature of adaptability has behind it some historical background. It closely depends upon the natural conditions of the habitat of a given species. For example, Gause (1939) and Smaragdova (1940) recorded that *Paramecium caudatum* and *P. aurelia* more readily adapt themselves to increased salinity than does *P. bursaria*. Two former species easily acclimatize themselves to 0.4%-0.6% salinity while increase of salinity over 0.21% is usually fatal to *P. bursaria*. It is

probable that the weak adaptability of *P. bursaria* to increased salinity is due to the fact that it usually dwells in peat bogs, where the concentration of electrolytes is very low.

It would be interesting to analyze the mechanism of the adaptive process in a case in which the part played by adaptive modification in the total value of adaptation is rather low, and in which the leading role belongs to the value of casual initial resistance. With that purpose we turned to the action upon Protozoa of such chemical factors which probably were never met with by them in their natural habitats. In this case strong adaptability is not to be expected.

Such new factors are presented by the action of various drugs on Protozoa. Quinine and arsenic preparations are widely used to cure diseases caused by pathogenic Protozoa. They are repeatedly introduced into the infected organism, and it is often observed that parasites acclimatize to their action and are no longer susceptible to the drugs in usual doses. Ehrlich recorded this process in his work with arsenic compounds. Whether this acclimatization of pathogenic Protozoa to the action of drugs is due to the natural selection of the more resistant strains of parasite in the course of the treatment, or whether it depends on the formation of adaptive modifications on the part of all the parasites, is not known.

We attempted to elucidate such relations by studying the action of quinine upon various strains of *Paramecium caudatum* (Gause and Smaragdova, 1939). *Paramecia* were acclimatized to living in rising concentrations of quinine hydrochloride, added to their standard nutritive fluid. In the first month the concentration of quinine was brought to 0.0036%¹ (through the intermediary stages of 0.0009%, 0.0018% and 0.0027%) and in the second month to 0.0063% (through intermediary dilutions of 0.0045% and 0.0054%). The method of testing the initial and acquired resistance to quinine in each separate clone was identical with that employed in experiments with acclimatization to salinity.

Fig. 8 shows the distribution of resistances to quinine before and after acclimatization to 0.0036% solution in various clones of *Paramecium caudatum*. The test was made on the 30th day after

¹The dynamics of acclimatizing *Paramecia* to quinine was equalized with that employed in the experiments with salts. The concentration of 0.0036% of quinine and 0.36% of salts are the approximate resistances of non-adapted individuals of *P. caudatum*. Such concentrations of chemicals in the nutritive medium were reached in a month through three equally distributed intermediary stages.

the beginning of the experiment. Fig. 8 makes it evident that casual inherent diversities between separate clones of *Paramecium* in respect to quinine resistance before acclimatization are rather considerable as compared to the relatively slight capacity for modification which is observed.

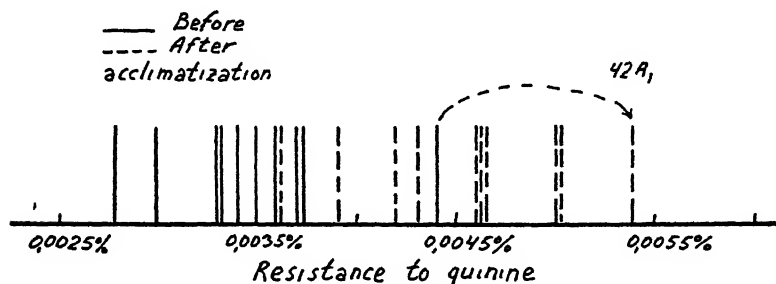


FIG. 8. Resistance to solutions of quinine in various clones of *Paramecium caudatum* before and after acclimatization. From Gause (1940b).

In the case of quinine, adaptability will evidently not play any leading role in natural selection. The most useful condition appears to be the combination of the powerful initial adaptation with the relatively moderate adaptive modification. Such, for example, are the properties of the clone 42a₁. Its total resistance attains 0.0054%. Combinations of weaker initial adaptation with the more powerful adaptive modifications yield smaller values of the total resistance (0.0050%; 0.0047%; 0.0044%). Combinations of powerful initial resistance with great adaptability are again absent.

Summarizing, it can be stated that the acclimatization of *Paramecia* to quinine is essentially different from their acclimatization to salinity. In the case of quinine the conditions are favourable to selection for casual initial strength of resistance accompanied by relatively moderate adaptability. At the same time in the acclimatization of *Paramecia* to increasing salinity a selection is inevitable for strong adaptability accompanied by weak initial strength.

It is rather remarkable that the adaptation of an animal to changing environment may lead to two consequences which are directly opposite to each other. In the case of a plastic animal, or of a normal variable in the environment, such as the salinity, the adaptation to changing conditions will only further enhance its plasticity by means of natural selection. But in specialized animals, or artificial

factors in the environment, such as quinine solutions, the adaptation to changing conditions may at the beginning only further reduce the plasticity and increase specialization.

The danger of an early increase in specialization in a changing environment is clearly manifest as soon as we look at the further destiny of such animals under conditions which continue changing. With the further increase of concentration of quinine in the surrounding medium, the absolute value of adaptive modification in various clones of *Paramecium caudatum* is increased. The non-specialized but plastic clones of infusoria, which at the beginning of the adaptive process were deficient in resistance and so doomed to extinction from the mixed population (their total resistance was only 0.0044% against 0.0054% for the specialized clones) with the further adaptation to rising quinine concentrations in pure cultures so strongly compensate their weakness that finally they get ahead of all other clones (0.0109% against 0.0091%). In contrast to this, the specialized clones which had the initial advantage, fall behind other strains in the course of continued growth of the absolute value of physiological modification.

It is hence evident that if natural selection fixes in mixed population in the early stage of an adaptive process to a changing environment, a specialized but non-plastic form (such as, for example, the clone 42a₁ of *Paramecium caudatum*), it inevitably prepares the subsequent disappearance of this form in the course of the further change of environment. The specialized form will at some time be unable to compete with such potentially more powerful non-specialized races as could occasionally survive in surrounding habitats.

It appears highly remarkable that the generalizations of palaeontologists, arrived at in the course of studies of long-range evolutionary trends, can be directly observed and accurately measured in the case of micro-evolutionary adaptation of *Paramecia* to different culture conditions. The details of these experiments, as well as the records of original observations, were already published by Gause (1942) and need not be repeated here.

3. ILLUSTRATIVE EXAMPLES.

The principle of compensatory relation between phenotypic plasticity and genotypic specialization in a group of closely related races or species appears to have a rather wide application. First of all,

this principle holds true not only for the physiological, but also for the morphological characteristics of ciliates. Fig. 9 represents the relation between the body surface in various races of *Paramecium bursaria*, and the modification of that surface acquired under the action of the increased salinity of 0.2%. In the case of a great inherent body surface of a given race of *Paramecium*, the surface

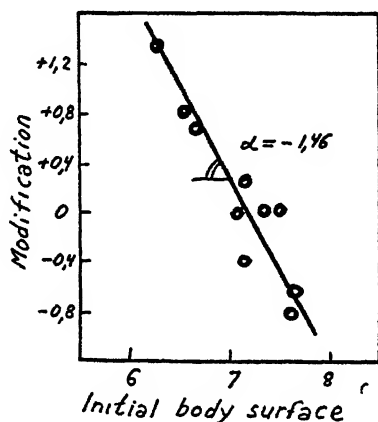


FIG. 9. The relation between the body surface in various clones of *Paramecium bursaria* and the modification of that surface under the action of increased salinity of 0.2%.

somewhat decreases under the effect of salinity, whereas in the inherently smaller races the surface increases. To conclude, we are again met with the compensatory relation between the inherent body size and the magnitude of the acquired modification of that size.

The relation of modifications to inherent diversities is very interesting, and it certainly should be studied also in animals other than Protozoa.¹ A few other examples will be given for the purpose of illustration.

Kalabukhov (1937) studied adaptation of the blood of forest mice to a mountain environment. At high altitudes oxygen tension is lower than on the plain. It is well known that the blood of mammals is very sensitive to decreased oxygen tension. In order to provide the supply of oxygen to the tissues under conditions of oxygen-deficiency in the atmosphere, the number of erythrocytes and

¹ Modification under the action of increased salinity in a clone of vegetatively reproducing infusoria biologically corresponds to the process of ontogenic adaptability in multicellular animals.

the haemoglobin-content of the blood are increased. It is only variation in the number of erythrocytes that will be considered here.

Kalabukhov studied several species of mice belonging to the genus *Apodemus* and including *A. sylvaticus*, *A. flavicollis* and *A. agrarius*. Experimental transportation of mice from the plain into the mountains has shown that at high altitudes the number of erythrocytes in the blood of *Apodemus sylvaticus* considerably increases in comparison with the initial number. This species acclimatizes well to high altitudes. The behaviour of the other species, *Apodemus agrarius*, is quite different. When simultaneously transported from plain into mountains, the number of erythrocytes in the blood of this species increases so insignificantly that it does not provide a proper supply of oxygen to the tissues. Due to such a weak capacity for formation of modifications, this species cannot survive transportation to high altitude and rapidly dies out. Table 5 gives some comparative data on the alteration of the number of erythrocytes in *Apodemus sylvaticus*, *A. agrarius* and *A. flavicollis*.

TABLE 5

Number of erythrocytes in millions per mm³ in the blood of various species of mice on the plain and after their elevation to high altitude.

Data of Kalabukhov (1937).

Species	Initial number of erythrocytes on the plain	The final number of erythrocytes at high altitude	The increase of the number of erythrocytes (modification)
I. Transportation to high altitude			
1. <i>Apodemus sylvaticus</i>	8.6	9.4	+ 0.8
2. <i>A. agrarius</i>	9.3	9.4	+ 0.1
II. Prolonged action of artificially decreased atmospheric pressure			
1. <i>A. sylvaticus</i>	8.4	9.2	+ 0.8
2. <i>A. agrarius</i>	10.6	9.0	- 1.6
3. <i>A. flavicollis</i>	7.5	9.5	+ 2.0

It can be seen that when the initial number of erythrocytes is great, this character does not give any significant adaptive modification. Such is the case in *Apodemus agrarius*. In the experiments

with artificially reduced atmospheric pressure the number of erythrocytes in this species even somewhat decreases. However, when the initial number of erythrocytes is small the magnitude of its further adaptive increase is rather considerable (*A. sylvaticus* and *A. flavicollis*). The final number of erythrocytes, or in other terms the total value of the adaptive feature of organisation, again appear to be more or less constant within the limits of the genus *Apodemus*. One again comes across a strong inverse relation between the value

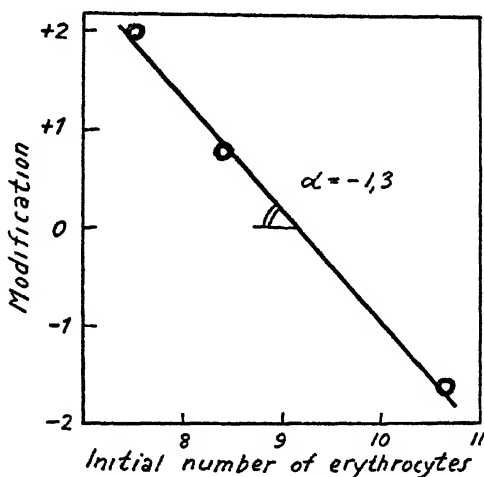


FIG. 10. The relation between the initial number of erythrocytes in the blood of various species of mice on the plain and the modification of that number under the action of decreased atmospheric pressure. Data of Kalabukhov (1937). From Gause (1940b).

of initial adaptation and the magnitude of acquired modification, which is represented graphically in Fig. 10. One gets the impression that there exists a certain maximal possible number of erythrocytes in the blood of mice of the genus *Apodemus*. The species *A. agrarius* possesses this maximal number on the plain. At the time of elevation to higher altitudes the number of erythrocytes has so-to-say nowhere to expand, the adaptive modification is not formed and this species perishes. In *A. sylvaticus*, however, the number of erythrocytes is remote from this maximal possible value. Hence this species possesses sufficient potentialities for adaptive modification.

Another interesting example is provided by the experimental data

published by Borsook (1942). She studied the consumption of oxygen by three different decapods: *Hyas*, *Eupagurus* and *Eualis*. The consumption of O_2 was at first measured in ordinary sea-water, and subsequently after a slow acclimatization to a gradual decrease of oxygen content, which was extended over a period of 7-8 days. Both *Hyas* and *Eupagurus* tolerate the decrease of oxygen content well, and their oxygen consumption is correspondingly decreased. The observations of Borsook were plotted by us in Fig. 11. Sepa-

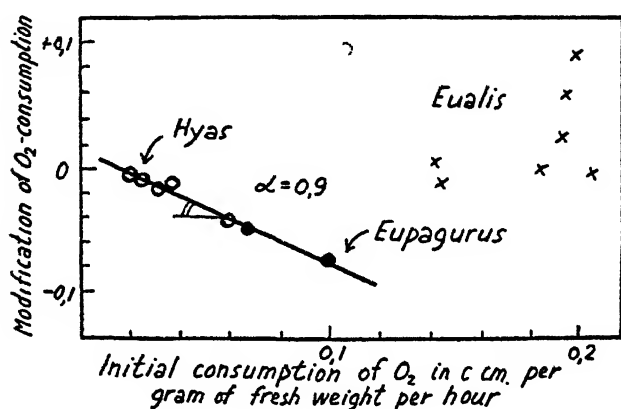


FIG. 11. The relation between the initial consumption of O_2 in different individuals of three species of decapods (*Hyas*, *Eupagurus* and *Eualis*) and the decrease in O_2 consumption after acclimatization to reduced oxygen tension. Data of Borsook (1942).

rate points represent here the data for different individuals. It is clear that the greater the initial consumption of O_2 by a given individual, the stronger is the decrease after acclimatization. In other words, the amount of modification is again bound by a compensatory relation with the initial state of a biological system. The observations for *Hyas* and *Eupagurus* lie along the same straight line, and in this way generic diversities differ here only in magnitude but not in kind from those observed within a single species. Both genera belong to the same physiological system. In distinction from this, *Eualis* are unable to acclimatize themselves to a reduced concentration of oxygen, and to diminish the consumption of O_2 . They evidently belong to another physiological system.

IV. THE PRINCIPLE OF COMPENSATORY RELATION BETWEEN ACQUIRED CHARACTERS AND INITIAL PROPERTIES.

1. GENERALIZATIONS.

In the preceding chapter experimental researches have led us to conclude that the magnitude of adaptive modification depends upon the amount of genoadaptation already attained. Gause and Alpatov (1941) and Alpatov (1944) suggested for the first time that this phenomenon can be generalized still further, and brought into agreement with compensatory relation between acquired characters and initial properties as observed in various living systems.

Although the principle of compensation in biology was enunciated by Geoffroy St. Hilaire more than a hundred years ago, it is relatively neglected in modern thought. Gause (1945) made an attempt to show that compensatory relation between acquired characters and initial properties holds true for numerous accurately recorded measurements in the fields of physiology and of experimental medicine.

To begin with, let us consider the following example. Vladimirov working in the field of aviation medicine has shown that living in mountains considerably raises the resistance of the human organism to reduced barometric pressure. When he measured the maximal reduction of pressure that can be tolerated by a given person before and after living in mountains, the following data were obtained (Table 6).

TABLE 6

Maximal altitudes (in meters) tolerated by different persons before and after living in mountains. Data of Vladimirov as reported by Kulikovsky (1941).

Observation	Before	After	Increase
1	7930	8700	+ 770
2	7870	8620	+ 750
3	7320	8800	+1480
4	6150	8600	+2450
5	8990	8640	— 350
6	7970	8770	+ 800
7	7570	8660	+1090
8	8180	8830	+ 650

The data of this table are presented by us graphically in Fig. 12. On abscissae are plotted initial resistances to reduced barometric pressure in various individuals, and on ordinates the acquired resistance after living in mountains. It is clear that these two variables are bound by an inverse relation: the less is the initial resistance of a given person, the greater is the acquired one. The person who was weakest before training (No. 4) yielded the greatest increase (+2450), whereas in the initially stronger persons the increase of resistance was less. Separate observations lie exactly along a straight

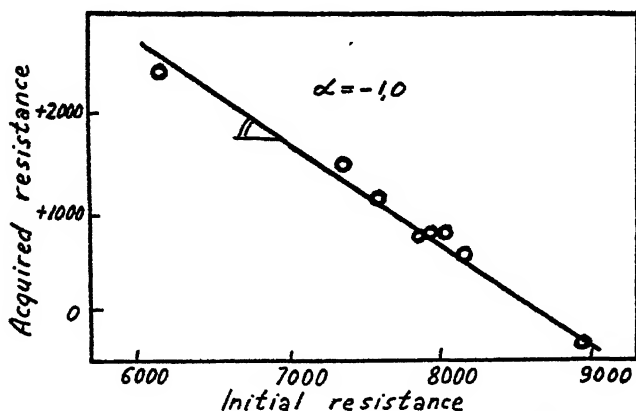


FIG. 12. The relation between the initial resistance to reduced barometric pressure and the acquired resistance after living in mountains, in various individuals. Data of Kulikovskiy (1941).

line. It is important to note that maximal tolerated altitude after training in all persons approaches 8700.

The following three generalizations can be deduced easily from experimental observations:

First generalization. When a heterogeneous group of individuals, whose members differ in the initial magnitude of some of their properties, is subjected to some external influence, the acquired alteration is the greater the less is the initial value of a given property in a given individual.

Second generalization. The decrease of acquirement per unit of increase in the initial property represents a fixed value, and does not depend upon the absolute magnitude of the initial property. This directly follows from the rectilinear relation between acquired and

initial properties. Fig. 12 shows that with the increase in the initial resistance from 6000 to 7000, the acquired resistance diminishes from 2700 to 1700; in the interval 7000-8000 correspondingly from 1700 to 700 and, finally, in the interval 8000-9000 from +700 to -300. The coefficient expressing the decrease of acquirement per unit of increase in the initial property can be calculated from the slope of the straight line drawn on Fig. 12. This coefficient (α) in the case considered equals unity.

This example shows that under fixed action of some external force upon living systems the amount of change of any single system depends on its initial state. A system resists alteration, and this resistance is the stronger the greater the magnitude of a given property attained in the initial state, before the application of external force. The decrease of acquirement per unit of increase in the initial property (α)¹ can be termed the *specific resistance* of an organism, or biological system. With the aid of this term our second generalization can be written thus: *the specific resistance of a biological system maintains a fixed value during any constant action of an external force.*

Third generalization. The specific resistance increases with the increase in the intensity of the external action. When the same group of individuals is studied after some slight external influence at the time t_1 , and later after a stronger action at t_2 , the specific resistance being in each case a constant value, will be in t_2 greater than in t_1 .

This generalization directly follows from the experimental observations. We have already noticed in the data presented in Chapter 3 (Fig. 6) that $\alpha_1 = 2.0$ and $\alpha_2 = 3.6$ and that $\alpha_2 > \alpha_1$. Let us outline here in some detail another example from physiology.

Fomichev (1939) studied the effect of forced increase of respiration upon the pulse rate. The observations were made on healthy, well trained men aged 19 to 25 years. After a prolonged rest in the laboratory, in the morning, before taking a meal, these persons made forced respirations through a gas watch. The rate of respiration was given by a metronome. To maintain a fixed intensity of respiration throughout the experiment, every person controlled the depth of respiration by observing the arrow of the

¹ Although the slope of the line is negative, α is regarded as a positive number. Ed.

gas watch. The results of these experiments are presented in Fig. 13. On the abscissae are plotted initial pulse-rates at rest in three individuals kept under observation, and on the ordinates the increase of pulse-rate after five minutes of forced respiration. It is clear that the increase of pulse-rate is the less, the greater the

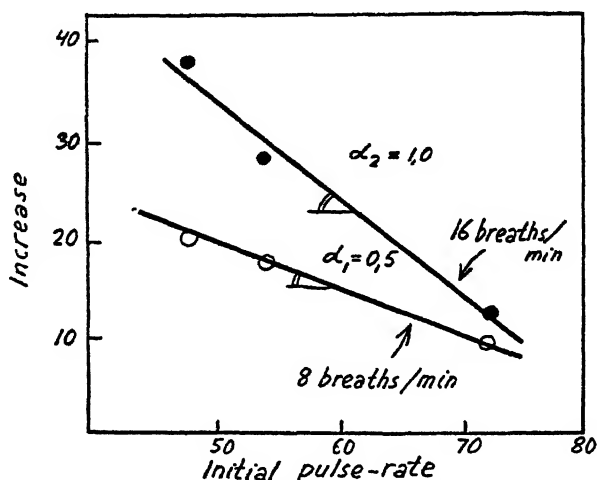


FIG. 13. The relation between the initial pulse-rate at rest and the increase in pulse-rate after forced respirations, in three different persons. Data of Fomichev (1939).

initial rate of pulse at rest. With slight intensity of forced respiration (8 breaths per minute) the coefficient of specific resistance $\alpha_1 = 0.5$. Under doubled intensity of respiration (16 breaths per minute) $\alpha_2 = 1.0$. It is important to note that $\alpha_2 > \alpha_1$.

2. EXAMPLES FROM PHYSIOLOGY.

It was shown by Gause (1945) that the generalizations referred to above hold true for numerous cases in the fields of physiology and of experimental medicine. Only two more examples will be given here, and some other data summarized in the form of a table.

Schazillo (1926) stated that potassium content in the blood of arthritic persons considerably increases after a number of mineral baths. Plotting his data on the graph one can see that the lower is the initial content of potassium, the stronger is the increase (Fig. 14).

The following example demonstrates the compensatory character of the relation between acquired and initial properties. Krestownikoff

(1930) measured the chloride content in the urine of 24 sportsmen before and after a 28 kilometer race. It was found that in persons with low initial content of chlorides the concentration of the latter somewhat increases after the race, but in persons with the high initial

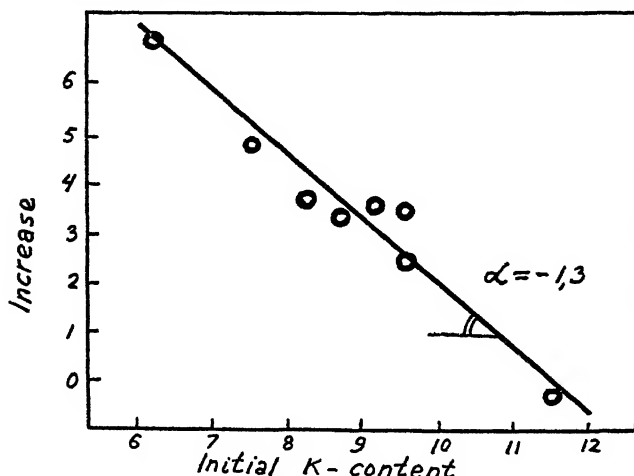


FIG. 14. The relation between the initial potassium content in the blood of arthritic persons and the increase of that content after a number of mineral baths, in various individuals. Data of Schazillo (1926).

content of chlorides the concentration of the latter strongly decreases (Fig. 15). The separate observations scatter along a straight line with the coefficient $\alpha = 1.2$.

Table 7 summarizes some further examples in this field.

TABLE 7

Compensatory relations between acquired characters and initial properties
From Gause (1945).

Initial property	Acquirement	Coefficient α	Authority
1. The consumption of O_2 at 12° while driving a bicycle ergometer	Increase (or decrease) at 34°	0.23	Dill (1931)
2. The consumption of O_2	Increase after a small dose of cocaine	0.95	Herbst and Shellenberg (1931)
3. The pulse rate at 12° while driving a bicycle ergometer	Increase at 34°	1.05	Dill (1931)
4. Number of leucocytes in the blood	Decrease after feeding lecithine	0.5	Atzler and Lehmann (1936)

As numerous other examples have been already reported in detail by Gause (1945), they will not be repeated here.

3. THE ANALYSIS OF TRAINING.

An analysis of compensatory relations between acquired characters and initial properties has led us to embark into the realm of physiol-

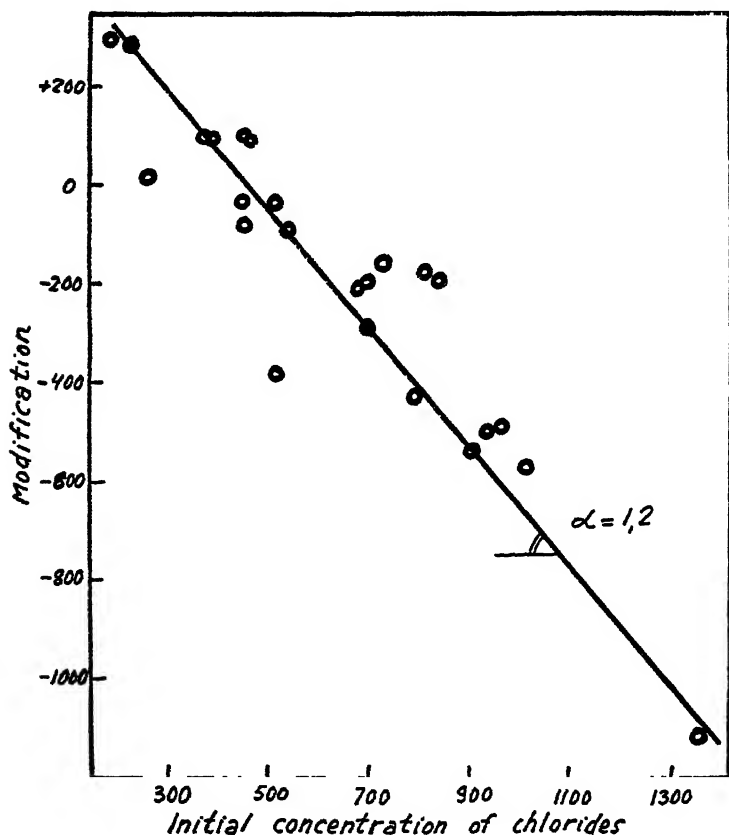


FIG. 15. The relation between the concentration of chlorides in the urine before a race and the change of that concentration after a race, in various individuals. Data of Krestownikoff (1930).

ogy, and it would perhaps be appropriate to end our discussion by consideration of compensatory relations in their dynamic aspect, which in this particular sphere is known as the analysis of training.

It is recognized that every exercise gives at first rapid advance and afterwards a slower one. The process of training can be expressed mathematically with the aid of a saturation curve. The rate of training of every individual (dy/dt) is proportionate to a difference between the physiological limit of attainment (y_{lim}) and a current attainment (y):

$$dy/dt = \alpha (y_{lim} - y) \dots\dots\dots (1)$$

This equation was already used in the analysis of training by Schukarev (1907), Henry (1911), Spielrein (1925), Ertlinger (1926), Heinis (1928), Husband (1931) and Gulliksen (1934); the latter gives a complete review of the subject. It is a characteristic feature of the equation (1) that a change in some specific property of the organism per unit of time (dy/dt) linearly decreases with the increase in the absolute magnitude of that property (y):

$$dy/dt = \alpha y_{lim} - \alpha y.$$

If we now transfer this general property of training from individual exercise to the training of a heterogeneous group of individuals it will be clear that weaker persons starting their training from lower levels will manifest more advance per unit of time. The initial advance of a weak person falls upon an easy part of the curve of training, inasmuch as the difference between the physiological limit of attainment and the current attainment is here sufficiently great. In distinction from this, the advance of a stronger person is associated with the movement along a more difficult part of the training curve. As far as experiments always reveal a linear negative relation between acquired (dy/dt) and initial (y) properties of organisms, it means that the equation of saturation (1) holds true not only for individual training, but also for a change in a group of individuals under the action of some training or some influence. Alpatov (1944) also noted the regularity.

We are now approaching a subject of the greatest importance for the problem under investigation. What is the relation between the individual curve of training of a given person and the effect of training upon a heterogeneous group of individuals? Fig. 16 (1) represents the essence of this relation. We plotted here the data of Fomichev (1939) concerning the effect of forced respiration upon the pulse-rate, which were referred to in section 1 of this Chapter.

Fig. 16 gives individual curves of increase in pulse-rate with time under the action of 8 forced breaths per minute in three subjects kept under observation. These three subjects were kept under absolutely identical conditions both at the time of experiment and before it. They were healthy men of similar age. It is probable that the difference in their reactions were due to constitutional factors. Sub-

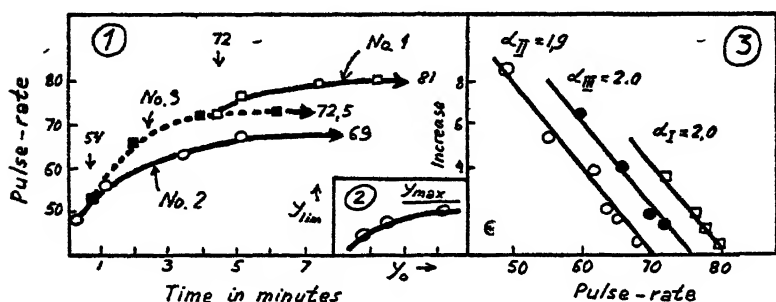


FIG. 16 (1). Individual curves of change in pulse-rate with time in three subjects. (2) The dependence of y_{lim} upon y_0 . (3) The individual dependence of increase in the rate of pulse upon current rate of pulse. From Gause (1945).

ject no. 2 showed the lowest pulse-rate at rest, equal to 42; under the effect of forced respiration this rate raised following a saturation curve and attained 69. Subject no. 3 had the rate of pulse at rest equal to 54. Plotting this ordinate upon the corresponding curve for subject no. 2 we can see that further rise of pulse-rate under forced respiration in subject no. 3 does not coincide with those for no. 2; starting from a higher level he attains a higher physiological limit ($72\frac{1}{2}$). Correspondingly, subject no. 1 starting from the pulse rate at rest equal to 72 attains the highest limit (81).

Fig. 16 (1) shows that individual curves of training of different persons follow different paths: one has to do here not with a *single* curve, but with a *family of curves*. In other words, the initial and acquired components of a given property are not interchangeable. When a high initial pulse-rate of a given person depends upon constitutional factors and is observed at rest, it can be raised to a higher level under the effect of training as compared to that of a person with the low initial pulse-rate.

It is clear that the limit of pulse-rate attained in the course of

training (y_{lim}) is not fixed, but depends upon the initial rate of pulse at rest (y_0):

$$y_{lim} = f(y_0)$$

The character of this dependence, on the basis of Fomichev's data, is presented in Fig. 16 (2). With the rise of y_0 the value y_{lim} approaches maximal value (y_{max}) again by the law of saturation, so that

$$y_{lim} = y_{max} (1 - e^{-by_0}) \dots\dots\dots (2)$$

Inserting the expression (2) into equation (1) we obtain the equation of a family of curves of training, showing the dynamics of this process as a function of the initial state of a given individual at rest (y_0) and its properties at a given moment of time (y):

$$dy/dt = a [y_{max} (1 - e^{-by_0}) - y] \dots\dots\dots (3)$$

For calculation of *individual* coefficients of increase in the rate of pulse of every person (a_1, a_2 , etc.) we can plot on abscissae the rate of pulse in a given person at a given time, and on ordinates the corresponding increase in the rate of pulse per unit of time (one minute). These recalculations are also presented in Fig. 16 (3). Although three experimental subjects possessed different rates of pulse at rest and different limiting values of pulse-rate at work, the coefficients of *individual increase* in the rate of pulse (a_1, a_2 , etc.) are in them practically identical and close to 2.0. These observations well agree with the equation (3) in so far as the differences in the initial state (y_0) as written in this equation do not affect the slope of the straight line relating dy/dt with y in the individual training.

It is reasonable to conclude that the family of the curves of training given by us above well reflects the compensatory relations between acquired characters and initial properties in their dynamic aspect.

Although the principle of compensatory relation between acquired characters and initial properties holds true for a great variety of cases, the details of these compensations are so diverse that it is certainly impossible to cover all of them by a single family of curves.

There are cases when high initial values of some characters, although yielding moderate increments, are nevertheless raised to higher final levels than the low initial values under the same change of external force (Figs. 8 and 16). In some other cases low initial values acquire such great increments that they far out-distance high initial values in their total magnitudes (Fig. 6). And finally, sometimes the compensation is a complete one (Figs. 5 and 12). In these three different situations the greater the acquired alteration the less is the initial value of a given property in a given individual, but the differences in the final levels reached may contribute to important differences in the direction of evolutionary process.

V. CONCLUSIONS.

It remains for us to reconstruct the train of thoughts which have led us in the present work, and to attempt to achieve an outlook for the future. About 50 years ago Baldwin, Osborn and Lloyd Morgan advanced the concept of organic selection, i.e. the substitution of adaptive modifications by adaptive mutations with the aid of a selective process. But this concept was evidently premature: at that time most biologists were still convinced of the heredity of acquired characters and the new idea was for them merely a superfluous one. It did not induce anyone to start experimental investigations and so it came to a dead end; organic selection was practically forgotten.

An independent statement of the same concept was made in Russia and is associated with the names of Lukin, Schmalhausen and Kirpitchenkov. At the time of renewed theoretic activity in this field, about 1936, the heredity of acquired characters was already disproved by experimental research. So there was no alternative explanation for many parallelisms between modifications and inherent diversities, and the old idea of organic selection shone with a new light. At this time it induced a number of investigators to attempt to verify the concept by experimental research.

The advances in genetics of Protozoa made it possible to undertake these studies on unicellular animals. It was found that in some cases organic selection actually occurs, but it was also noted that the possibilities of genotypic response to the change of environment are much wider than the possibilities of phenotypic response. The adaptation to some slight alteration in temperature or in salinity

may happen at first by adaptive modification, which is later replaced by the more powerful genoadaptation. The degree of resemblance of genoadaptation to phenoadaptation, however, may not be a very great one. But when an organism has to enter a more drastically changed environment, direct natural selection of genoadaptations will be inevitable, and a preparatory stage of modificational change may not be observed. These conclusions are based upon the experimental investigations of adaptation in infusoria, mainly in *Paramecium* and in *Euploes*.

In the course of these studies it was discovered that among different races of the same species the amount of modificational change depends upon the amount of genoadaptation already attained. These two features of organization are not independent, but are bound by a compensatory relation: the less the genoadaptation, the greater is the adaptive modification, and vice versa.

If adaptive modification and genoadaptation be considered as equivalents, in the field of micro-evolution, to the plasticity and specialization usually considered by palaeontologists in the long-range evolutionary trends, it becomes possible to observe in the laboratory an inverse relationship between plasticity and specialization, and to see how this relationship plays its role under various conditions of adaptation. We have in fact observed many such interesting situations under laboratory conditions.

An inverse relation of phenotypic plasticity to genotypic specialization among different races of the same species evidently depends upon the organizations of living systems, and represents a special case of the more general principle of compensatory relation between acquired characters and initial properties of organisms as it was noticed for the first time by Gause and Alpatov in 1941. It is the consideration of this latter principle that brought us into the realm of physiology, and convinced us of the validity of compensatory relation for many physiological examples.

We hope that this line of thoughts and investigations will not come to a dead end again. We wish it to be taken by a number of independent investigators, to be elaborated and further advanced by means of experimental investigations. It should perhaps be supported by, and contribute to, the growing body of physiological genetics. It can perhaps be considered as an important beginning of the new trend in biology.

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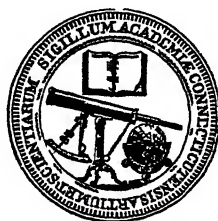
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A Study of Palaeozoic Arachnida

BY

ALEXANDER PETRUNKEVITCH



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A STUDY OF THE STRUCTURE, CLASSIFICATION
AND RELATIONSHIPS OF THE
PALAEOZOIC ARACHNIDA

based on the collections of the British Museum

by

ALEXANDER PETRUNKEVITCH

Professor of Zoology, Emeritus, Yale University

(A Contribution from the Osborn Zoological Laboratory)

*This Study is dedicated
to my colleagues and associates
in the Osborn Zoological Laboratory
in sincere appreciation of their encouragement
of my work after my retirement from active duty.*

(Submitted for publication January 1948)

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A STUDY OF PALAEOZOIC ARACHNIDA

INTRODUCTION

The great advance in our knowledge of the comparative internal anatomy, development and neurology of Recent Arachnida and of other related groups of Arthropoda during the past fifty years opened new avenues of approach to their study by making correlation of their external features with the rest of their organization not only possible, but imperative. No more can mere reshuffling of taxonomic units on the basis of external characters alone be accepted as an adequate reason for a new "natural" classification, unless other important characters involving fundamental anatomical and embryological features fall in line and furnish the required corroborative evidence. External resemblances, when unsupported by such evidence, are often quite deceptive. This is particularly true in the case of such arthropods as Crustacea, but applies to Arachnida as well. On the other hand, great external differences may be exhibited by closely related groups. To be sure, identification of species, genera and families, and to a certain extent of even higher taxonomic units of arthropods has in the past always depended upon externally visible structures and will continue to depend upon them in the future, unless one is prepared to sacrifice the specimens for a study of their internal anatomy. But the choice of such characters and their use must be regarded merely in the light of their utility, not in themselves indicative of fundamental differences. One should not belittle their practical value, but at the same time should not exaggerate their phylogenetic importance.

The student of fossil Arachnida has no other alternative than the use of external characters, because internal organs are scarcely ever preserved and then only very imperfectly. When it becomes necessary to correlate the external features of fossils belonging to extinct orders, this can be done only by reference to similar structures found in now living Arachnida of other orders. In other words, in case of fossils we have to depend upon analogies. This in itself requires great circumspection. But additional, often serious difficulties arise owing to imperfect preservation, distortion, superimpression and scarcity of material. As we shall see further, misinterpretation of visible structures happened repeatedly even on the part of distinguished investiga-

tors thoroughly familiar with arachnology. It is in the hope of helping to avoid such misinterpretations in the future that I propose to discuss next the value of external characters in the study of fossil Arachnida.

General Remarks Concerning Fossil Arachnida

Although one meets constantly with the statement that in Palaeozoic Arachnida we deal with molds of external surfaces, this is only partially true. It is an old experience that some structures of a specimen may be molds, while other structures are casts. That is particularly true of the eyes which often appear as little concave bowls and occasionally as convex hemispheres. It is probable that in the latter case we have before us not a cast, but the fossilized lens itself, chemically changed in the course of time. Sometimes the rest of the chitinous layer of the body wall is still preserved at least in patches. In that case the true mold of the external surface is concealed. But if the chitinous layer became chemically changed, like the convex lens, then we are looking not at a mold of the outside, but at the interior surface of the body wall, which is different in appearance from the outside surface, as one can easily ascertain by examining a now living arachnid. In fact, my own experience shows that the latter case is as common as the former. In interpreting such pictures it is necessary to bear this fact in mind, especially in the case of the coxae. In case of living Arachnida the picture of the arrangement of the coxae, when one examines them from the outside, is usually strikingly different from that presented by the inner surface of the ventral wall.

When chitin is preserved on the appendages we may be seeing its outside surface, as in some cases of the hands of scorpions, or more commonly the lining of their inside cavity, because appendages are usually preserved as hollow tubes. Strange as it may seem, the inter-articular membranes of appendages are often fossilized as such. Similarly, in many cases the walls of the coxae are preserved as such, in which case their cavities present to the observer the inner surface. Usually adjoining walls of two coxae appear then as a single wall. In rare cases, as in some *Anthracomarti*, some muscles are also fossilized as such.

Distortion is very common and has been discussed many times by earlier investigators. Of special interest is the inversion of a convex surface, which is a common feature in the case of the dorsal abdominal wall in *Anthracomarti*.

In some specimens the same surface, usually the dorsal one, appears

on both pieces of a nodule. Both may be negative or one may be negative and the other positive, or one may be a mold of the outside and the other of the inside of the same wall. This is the case when the abdominal cavity became early filled out with mud which was later petrified. In such cases one should expect the existence of a mold of the inner surface of the opposite, i.e. of the ventral wall; the latter may be then exposed to view, as will be shown in the chapter on *Anthracomarti*, by removal of the matrix bearing the mold of the inner surface of the dorsal wall.

In cases of otherwise excellent preservation the most serious difficulty is presented by the superimpression on the same surface of lines and of other structures belonging to the opposite surface. The case of the *Anthracomarti* is particularly illustrative and interesting in this respect and will be dealt with further down.

Carapace

The structure of the carapace is of great importance in Arachnida and should be clearly understood. In three orders, Palpigradi, Schizomida and Solifugae, it is segmented, in all others it is entire. The latter condition does not mean that the cephalothorax as such is unsegmented. It means merely that its dorsal wall, the carapace, forms a single unit. It may still retain outward signs of embryonic segmentation in the shape of more or less distinct sulci or grooves, but it retains its unity in all postembryonic stages and in moulting is shed as a single, complete plate. It also retains its unit nature after death and appears as a single plate if severed from the abdomen, as happens to be the case in many fossils. Unfortunately, this fact, well known to professional arachnologists, seems to have been misunderstood by some paleontologists. Thus Pruvost in his fundamental work dealing with the French Carboniferous fossil fauna objects to my classification of 1913 in the case of the *Anthracomarti* because I do not take into account the "segmentation" of the cephalothorax (meaning the carapace) of the Family *Brachypygididae*, proposed by Pocock. Referring to the characters by which the *Brachypygididae* differ from the *Anthracomartidae* Pruvost says: "1° Le céphalothorax est segmenté, construit sur un type identique à celui des Eophrynidés." Their carapace is sculptured, but not segmented. Sculpturing is a common feature in many Recent and fossil Arachnida, but it has only generic value and in some spiders the carapace is sculptured only in one sex, as for example in *Arachnura feredayi* L. Koch, in which the carapace of the

female shows fairly deep thoracic sulci, while that of the male is uniformly convex.

A segmented carapace (Figures 3 and 4) consists of a single propeltidium, a paired mesopeltidium and a paired metapeltidium. These individual sclerites are separated from each other by soft membranes. The taxonomic value of a segmented carapace is of a higher order than that of an unsegmented one. The segmentation is retained in all species of the three orders possessing a segmented carapace. A segmented carapace has only once been described and figured in a fossil, namely by myself in *Protosolpuga carbonaria* in which it differs from the Recent type in being composed of three plates instead of five, the first presumably representing the propeltidium, the second the mesopeltidium and the third the metapeltidium. Although a fossil representative of the Order Palpigradi has been described from the Mesozoic and a representative of the Order Schizomida has been recently described by myself from the late Coenozoic of Arizona, the carapace of these fossils is not known.

A feature of great importance in living and fossil Xiphosura as well as in the extinct Class Eurypterida is the so-called doublure of the carapace, i.e. its ventral infolding. In the Class Arachnida a doublure exists only in the Order Thelyphonida (Figure 2). Here the carapace consists of a single piece. Viewed from above, the doublure is not visible (Figure 1). The sulci radiating from the oval depression of the thoracic apodeme are probably remnants of embryonic segmentation. In ventral view (Figure 2) the doublure is clearly visible (DB). As it forms a single plate with the rest of the carapace it remains with it as a unit in moulting. However, to see it properly one has to remove the carapace because the view of the doublure is greatly obstructed by the coxae of the powerfully developed pedipalpi. This is probably the reason why the doublure has never been seen in fossil Thelyphonida, nor ever was an object of search.

The Juncture between the Cephalothorax and the Abdomen

The importance of the type of juncture between the cephalothorax and the abdomen has been repeatedly pointed out by various investigators. In my article on Arachnida in the Encyclopaedia Britannica I tried to show its influence on evolutionary trends. The two extremes, i.e. broad juncture and juncture by means of a slender petiolus, are well represented by scorpions and spiders. But even in Recent Arachnida the juncture may be so concealed from view that only dissection

can settle the question as to which type it belongs to. Thus in all Ricinulei the true juncture is concealed and the abdomen looks as if it were broadly joined to the cephalothorax. Here the outwardly visible first tergite is, as dissection has shown, in reality the third tergite. The first and second tergites are concealed in the deep fold between the outwardly visible posterior edge of the carapace and the anterior edge of the abdomen. Because of other similarities of structure it seems safe to assume that in fossil Ricinulei the juncture is of the same type as in Recent ones.

The problem of juncture is, however, not as easily settled in the case of Arachnida belonging to extinct orders. Even when the posterior edge of the carapace is straight and as wide as the anterior edge of the abdomen, the appearance may yet be deceptive, as in the case of the Ricinulei. One has therefore to seek direct evidence that may be available in some exceptionally well preserved specimen. Occasionally, as in specimen No. 1552 of *Anthracosiro woodwardi*, shown in Figure 40 and photograph 247 the intersegmental muscles and the connecting membrane are preserved by a freak of nature. In other cases the carapace may have been severed from the abdomen after death, or an exuvium has been fossilized in which the carapace had been first split off in the process of moulting, thus exposing the true anterior edge of the abdomen. In the collection of the British Museum there are several specimens of *Anthracomarti* fossilized in this manner. In such cases (Figures 41 and 42 and photographs 204 and 205) the entire edge to which the connecting membrane was attached, is exposed to view. It is plainly visible because it has a slightly different structure and surface from the rest of the tergite. In other cases, the question of the type of juncture may be settled only by reference to the number of tergites and sternites. If it can be shown by superimposition of the two surfaces that the first visible tergite is the true first tergite, then species with a perfectly straight line separating the carapace from the abdomen as in some *Architarbi*, furnish fairly conclusive evidence of broad juncture, provided the line is not a double one.

Segmentation of the Abdomen

The original number of abdominal segments in all Arachnida is twelve. This has been proven by embryological evidence. But in adults twelve visible segments are found only in Thelyphonida, Schizomida, Phrynychida, liphistiomorph Aranaea, Pseudoscorpiones

and Scorpiones. It has been known for a long time that in scorpions the first abdominal somite disappears in the course of embryonic development. Later, as Buxton and I have shown independently, the first abdominal neuromere persists in the adult and the normal number of segments is restored by a subdivision of the eighth segment. The first visible tergite of an adult scorpion belongs, therefore, to the second embryonic somite, as does the first visible sternite with the genital opercula. In Recent scorpions the abdomen is accordingly composed not of twelve, but of only eleven embryonic somites, namely 2, 3, 4, 5, 6, 7, 8a, 8b, 9, 10, 11, 12, whereas in the other orders with twelve abdominal segments each segment corresponds to an embryonic somite. In Thelyphonida and Schizomida the last three segments are reduced to little annular sclerites forming the pygidium. In Phrynichida the pygidium is formed by the twelfth segment alone. In Pseudoscorpiones the twelfth segment is reduced to a tiny tergite and sternite. In *Liphistius* among the spiders all twelve segments are with a tergite and a sternite. It has been further demonstrated by numerous studies that in all Arachnida the genital opening belongs to the second abdominal somite and can be used, therefore, as a landmark for the determination of the true nature of any tergite and sternite, provided both the dorsal and the ventral abdominal walls of the same specimen are preserved. The student of fossil Arachnida is consequently confronted with several possibilities: there may be a loss of an entire first embryonic segment as in scorpions, or only the first sternite or tergite may be lost, or the first tergite may be in existence, but not visible, because it is hidden under the posterior end of the carapace, as already mentioned. Then there are the possibilities of subsegmentation as in the case of the eighth abdominal somite in scorpions and of fusion of adjoining sternites as in some Architarbi. Occasionally tergites also may fuse as in Ricinulei. Mere counting of tergites or sternites may be helpful in identification, but is misleading when it is necessary to establish homologies of segments and of corresponding organs, such as book-lungs. Superposition of the two surfaces is the safest method for the elucidation of the true segmentation when embryological evidence is lacking as in the majority of fossil arthropods, and unfortunately in all fossil Arachnida. Assuming that the tergites and sternites belong to the same somites when their lateral edges coincide, a reasonable assumption supported by embryological evidence, we can determine not

only their numerical value, but also whether subsegmentation or fusion has taken place. On the assumption that the complete set of twelve abdominal embryonic somites is a more primitive condition than one in which there is either a complete loss of the first somite or of one or more posterior somites, or one in which fusion or subsegmentation of somites may be demonstrated, an assumption supported by logic and facts, we may get a picture of evolutionary trends even when the latter do not become apparent in different orders of Arachnida in the same geological period. It also entitles us to disregard as completely fallacious and impossible such fantastic suggestions, as that of Fritsch, that attenuation of a scorpion's tail may be the first step in the formation of a thelyphonid whip, although he himself was not in favor of his own idea. Speaking of *Paleophonius loudonensis* Fritsch says "wenn die Glieder des Postabdomens wirklich so schmal wären (as shown in Laurie's figure, A.P.) dann hätten wir einen Uebergang zu den Theliphoniden vor uns, was sehr unwahrscheinlich ist." (p. 65). We shall discuss the problem of segmentation in detail in every order of Arachnida separately.

Arrangement of the Coxae

The arrangement of the coxae is of primary importance in Arachnida and for this reason is shown here in Figures 5 to 26 for every order of the class. It is probable, and is usually accepted, that in the ancestral, primitive arthropods the coxae were cylindrical, with both the sterno-coxal and coxo-trochanteral articulations circular, opposite to each other and at right angles to the axis of the limb. Coxae of that shape are never found in Arachnida. Even when the coxa itself is cylindrical, as in the case of the pedipalp and first leg in *Koenenia*, the sterno-coxal foramen is displaced dorsally. In the vast majority of Arachnida the coxae have lost their cylindrical shape in favor of a more or less conical one, opening into the cephalothorax by a considerable portion of their length. The movability of a coxa is therefore governed by a number of factors, one of which is the shape of the sterno-coxal foramen. When all coxae are far apart as in Palpigradi (Figure 13) their movability is naturally determined by the shape of that foramen alone, and although the extent of their motion may be small, they are rightly called movable.

When the coxae are in contact with each other, their movability

is not so easily determined. Thus in Phrynichida (Figure 17) all coxae of the same side are in contact with each other, yet they possess considerable mobility. On the other hand the third and fourth coxae of the same side in scorpions are always grown together. They can be moved only as a unit, although the cleft between them may be quite deep. The pedipalpal coxae in Thelyphorida not only are permanently united along the line of contact, but have lost their mesial wall so that the two coxae have a single, coxal cavity common to both of them. Viewed from below they appear as two separate coxae. Viewed from the inside, when the dorsal wall is removed, the remnant of the fused mesial walls appears as a small ridge.

This shows how difficult it is in the case of extinct Arachnida to decide whether their coxae are movable or immobile. In view of the fact that in some orders of Recent Arachnida there is considerable variation in this respect, furthermore in view of the fact that in some Arachnida some of the coxae are movable and others immobile in the same animal, the entire question of the movability of coxae may seem to be of little importance. This is not so. There are physiological reasons requiring movability, such as the presence of gnathobases and their use in the process of feeding, as in scorpions. There is always a set of muscles present in the cephalothorax for the purpose of moving each movable coxa. With immobile coxae such muscles are wanting. But even apart from their own movability or immobility the coxae are of necessity related to the disposition of other organs inside the cephalothorax. The knowledge of the disposition of the coxae is therefore not only helpful in classification, but of considerable importance. It serves as a restraint against taxonomic regrouping of arthropods merely on the basis of the movability or immobility of their coxae alone, with a disregard of all other characters, as has been attempted by Oudemans. Such grouping is in direct contradiction to available important evidence derived from the study of other organs. Any classification based on it is doomed to failure.

Considerable variation in the disposition of the coxae exists in every order of Arachnida as well as in other arthropods. Some of these variations will be dealt with in each order separately. One important feature must, however, be pointed out here, namely, that whatever the variation in the disposition of the coxae within the same order may be, their relation to the position of the mouth

in that order remains constant. It was this feature which induced me to create the new Subclass Stethostomata for two of the extinct orders.

Thoracic Sternal Plates

Most of the arachnid orders possess one or more sternal plates representing the sternites of the thoracic embryonic somites. Since in a typical arachnid there is always the same number of appendages behind the chelicerae, we may regard five as the maximum number of sternal plates. This number as yet has never been found in any Recent or fossil Arachnida. This is due partly to a fusion of the adjoining sternites, partly to their diminution in size connected with the degree of separation of opposite coxae of the same pair and of consecutive pairs of coxae. The law governing the disappearance of the sternal plates is different from that governing the disappearance of abdominal sternites. The most primitive condition is found in the Palpigradi. Here the pedipalpal and first pedal sternites are fused, forming a single large prosternal plate (Figure 13, st), while the following three segments retain each an independent and well defined sternite. In the Thelyphonida (Figure 14) we find a similar condition, but the second and third pedal sternites are reduced to minute sclerites. The metasternite on the other hand remains well developed and is intimately related to the type of juncture between the cephalothorax and abdomen, found in Thelyphonida. In the Schizomida (Figure 16) the second and third pedal sternites are completely wanting, crowded out by the contiguity of the third pair of coxae.

In Scorpiones the three anterior sternites are wanting, while the sternites of the third and fourth pedal somites are fused forming a single plate, except in the Family *Bothriuridae* in which the third pedal sternite has also disappeared, while the fourth is represented by a pair of narrow sclerites.

The metasternum, i.e. the sternal plate of the fourth pedal somite, presents an interesting problem in connection with the interpretation of some fossil arachnid segmentation. As we have just seen it is present in several Recent orders. It is usually more or less triangular in shape and occupies the space between the fourth coxae. When the latter are pyramidal or conical, especially if the coxae are contiguous at their apices, the triangular space is really formed by the posterior edges of the fourth coxae and the transverse inter-

segmental line between the cephalothorax and the abdomen. The first abdominal sternite may be reduced to a mere rudiment and hidden from view in the fold formed by the membranes in front of and behind it. In such a case (Figures 43 and 44) the metasternum may be easily mistaken for the first abdominal sternite. The triangular shape of the space enclosed between the fourth coxae is in itself not only no proof of its identity, but rather misleading, inasmuch as it is merely conditioned by the configuration of the coxae and may represent the metasternite or the first, second or even third abdominal sternite. Thus in *Liphustius* (Figure 18) it is undoubtedly the first abdominal sternite because the entire complement of twelve sternites is present and there is a corresponding number of tergites. In *Ricinulei* the triangle includes the first and second sternites and the limit between them is not easy to demonstrate. In *Opiliones* it is usually the second and third, or the third sternite alone (Figure 10). But what does it represent in such fossils as *Trigonotarbus johnsoni* (Figure 19) and *Architarbus minor* (Figure 12)? Only superposition of the dorsal and ventral surfaces of the same specimen can give a satisfactory answer and even then one must be on one's guard lest a segment concealed in a membranous fold escape observation. I have not been able to find any evidence of the existence of a metasternite in these fossils and on the other hand I found considerable evidence in favor of the triangle's being an abdominal sternite. We shall consider this matter again in its proper place.

Appendages

Thorough knowledge of all appendages in arthropods needs no emphasis. Unfortunately, what is so simple in now living *Arachnida* is far from being so in fossil species. Some reasons for this are self evident, such as the loss of appendages in the process of fossilization, their distortion or overlapping. Other reasons are not so apparent and must be seriously considered in order to avoid possible misinterpretation. Even the quite natural and general assumption that the segmentation of appendages in fossil species is the same as in their Recent relatives is something that can be substantiated only by direct comparison. In extinct orders the comparison of necessity must be made with more distantly related groups. It is then that difficulties arise. Thus, for example, the trochanter in some *Arachnida* is two-jointed instead of consisting of a single joint as in

the majority of orders. In recent Ricinulei the trochanter of the first and second pair of legs is single-jointed, that of the third and fourth pair two-jointed. That can be easily seen and the only problem in Recent Arachnida is the question as to the origin of the second joint. But in fossil Arachnida an intersegmental membrane may be easily mistaken for a segment. The fact that impressions of intersegmental membranes usually appear to be triangular because of the point of articulation of the segments, at which the membrane is exceedingly narrow, does not hold true in all cases. Subsegmentation of the tarsi is another point in question. It varies even in some Recent Arachnida, as for example in Opiliones. The presence of claws at the end of a joint would settle the question, but in Palaeozoic Arachnida, while known and figured, the claws themselves are very rarely and usually imperfectly preserved. Such a case of perfect preservation as shown photographically in Figure 199 is unique, as is also the case of *Eobuthus*, shown by Wills (144) in his Figure 1 on Plate 3. The case of *Palaeophonius* (*Proscorpius*) *osborni* shows how easy it is to mistake an unevenly broken end of a joint for a pair of claws.

Some appendages, namely the chelicerae and pedipalpi, are regularly hidden from view in several orders of Arachnida because of their anatomical position. That is the reason why these appendages have been so poorly known in Architarbi, Anthracomarti, etc. In such cases it is pure luck if one comes across a specimen exposed in a plane making these appendages visible.

Of abdominal appendages only the combs of scorpions are well known and figured in some fossil species. No structures have ever been seen in Palaeozoic spiders, which could be definitely identified as spinnerets, although they form the most characteristic feature of the Order Araneae and their absence, if proven, would necessitate the creation of a new order. Only Fritsch described and figured "genital appendages" in Palaeozoic spiders, but his figures and interpretations are very unsatisfactory and cannot be used as proof of the existence of these appendages.

Organs of Respiration

In Recent Arachnida, the lung openings and the book-lungs themselves are more or less plainly visible from the outside. Tracheal spiracles are more difficult to see even when their position is known and fully exposed to view. In some cases, as in Ricinulei, they are

hidden from view. Occasionally one can see in Recent Arachnida the larger trunks of the tracheal tubes, but more commonly the tracheal system becomes visible only after dissection or on microscopic sections. Ventral sacs, such as are found in Recent Palpigradi and Phrynichida are also invisible unless specially prepared for study. In fossil Arachnida even the lung-slits are very rarely preserved. The presence of book-lungs has been indicated in several cases, but not definitely proven. Again, as in the case of the claws, such specimens as are shown in the present paper in Figures 47, 48 and 101 and photographically in Figures 213, 214 and 232, are extremely rare. Even in Palaeozoic scorpions the book-lungs have never been seen and the lung-slits have been figured only by Fritsch whose interpretations of visible structures often remain very doubtful as to their correctness. The case of the spiracle described by Thorell and Lindström in the Silurian scorpion *Palaeophonus nuncius* and figured by them in Figures 1 and 13 shows how great may be the difference in the interpretation of the same structure by two equally distinguished and equally experienced arachnologists. For the structure referred to by its discoverers as a spiraculum and given as evidence of their contention that the species was an air-breathing arachnid, was by Pocock declared to be "a fortuitous crack in the integument" (1901, p. 305). Pocock did not see the original specimen, but as he "found no distinct traces of stigmata in the Scottish specimen" (p. 306) he came to the very definite conclusion that both species were aquatic, "lived in the sea, probably in shallow water" p. 306). I, too, have not seen the types of either *Palaeophonus nuncius* or *P. hunteri*, but an examination of Thorell and Lindström's figures with the help of a lens leads me to the conclusion that they are drawn from real spiracles and are not figments of the imagination in the presence of a fortuitous crack. Thorell and Lindström were exceedingly careful observers and the figures accompanying their memoir are marvels of technique in the minutest details. As we shall see later, there are plenty of other reasons in favor of the assumption that the species of *Palaeophonus* were terrestrial scorpions.

No tracheal spiracles have ever been seen in Palaeozoic Arachnida. Even in Baltic Amber (Oligocene) specimens they usually do not show. So far as I know I am the only investigator who has seen and figured tracheal spiracles and even so in only three species, *Paruroctea blauvelti* in 1942 and *Eogonium robustum* and *Anyphaena fuscata* in 1946.

My interpretation of the structures which I described in *Architarbi* as ventral sacs is, of course, subject to criticism. There is no direct evidence that they are eversible sacs. They do not resemble book-lungs. Their position agrees best with that of ventral sacs and I think that until evidence against my assumption is produced, my interpretation of these structures is reasonable.

Apodemes

Apodemes or invaginations of the body wall for the attachment of muscles are usually, though not always easily visible in Recent Arachnida. The best known apodeme is, of course, the dorsal thoracic one serving for the attachment of the dorsal dilator muscle of the gizzard. On the outside it appears as a fairly deep thoracic groove the shape of which is often of value in taxonomy. In fossils it is often quite well visible and undoubtedly served the same purpose, so that the existence of the gizzard in Palaeozoic Arachnida may be considered as certain. Until the present no other apodemes have been observed in fossil Arachnida, perhaps because nobody looked for them. I have now found clearly preserved apodemes for the attachment of pulmonary muscles. They are shown in Figures 47 and 48. A comparison of these figures with Figures 45 and 46 showing similar apodemes in the common whipscorpion, *Mastigoproctus giganteus*, shows that their position in *Anthracomarti* was about the same as that in Recent Thelyphonida with the exception that there are three pairs in *Anthracomarti*, whereas there are only two pairs in Thelyphonida. The presence of a third pair of lungs in the former, visible in several specimens, explains the difference in their number and adds assurance to the interpretation of these elongated depressions as apodemes. Two apodemes are also visible in a photographic reproduction of the lungs in Figure 213. Unfortunately it is one of the most difficult subjects for photographic reproduction, partly because of the small size of the apodemes, partly because of their position requiring considerable tilting of the specimen in order to make them at all visible. In proper illumination under a binocular microscope the apodemes have very distinct outlines.

Shallow depressions of the chitinous body wall, serving for the attachment of dorso-ventral muscles are not usually considered as apodemes, but may nevertheless be mentioned here. Such attachment discs are well visible in the majority of Recent Arachnida, in the

abdomen. They are also plainly visible in some fossils where their function must have been the same. But in fossils one must be on one's guard against mistaking granules arranged segmentally, for muscular attachment discs.

Muscular System

The muscular system in Recent Arachnida is very complex and well known. Up to the present no muscles have been described in Palaeozoic Arachnida for the chief reason that muscles have not been preserved and partly because nobody was looking for them, the only exception being that of Peach (91) who shows in his figure 18c on Plate XXIII "a bundle of muscular fibres" in the digital joint of the palp of a scorpion. Where the apodemes and attachment discs are visible, the existence of the corresponding muscles may be safely assumed. Thus a well preserved specimen of *Geralinura gigantea* Petrunkevitch, belonging to Mr. George Langford of Joliet, Illinois, and courteously lent by him to me for study in 1945 shows four pairs of attachment discs on the second to fifth tergites, one pair for each tergite. It is possible that *Geralinura* possessed more than four pairs of dorso-ventral muscles, but it is quite certain that it possessed at least that many and on the segments mentioned. *Graeophonus carbonarius* (Scudder), specimen No. 37964' of the U.S. Nat. Museum figured in my Monograph (1913) on p. 68, has six pairs of attachment discs.

The appendages of fossil Arachnida resemble closely those of Recent species belonging to the same Order. In some specimens the articulations are plainly visible and warrant the assumption that the muscular system inside the appendages was represented by the same muscles.

Neither fossilized muscles nor fossilized muscle fibers have previously been observed in Palaeozoic Arachnida with the above mentioned exception of a scorpion described in 1929. I was, therefore, considerably surprised when I saw the dorsal muscle fibers connecting the carapace with the abdomen, well preserved and clearly visible in specimen No. 1552 of *Anihracosiro woodwardi* Pocock (Figure 40). The fibers are so well defined and diverge so symmetrically that there can be no mistake in the interpretation of the structure. It is not possible to interpret the picture as "fortuitous" folds of the intersegmental membrane itself, as it would not be possible to conceive a mechanical reason for such regular lines. It was even

possible to reproduce them photographically (Figure 247), although naturally they show much better when examined in proper lighting under a binocular microscope.

Another surprise was the discovery of structures which could be interpreted only as fossilized complete muscles. Since muscles in some Devonian sharks have been so well fossilized that Bashford Dean was able even to photograph their transverse striations, the fossilization of muscles in Palaeozoic arthropods does not seem to be outside of all possibility. On account of the hard, external skeleton preventing rapid penetration of the body by solutions and permitting autolysis of tissues before their fossilization, cases of fossilized arthropod internal organs are naturally very rare. In this connection I would like to recall to the memory of the reader that the complete absence of any internal organs in Baltic Amber arthropods was a generally accepted fact until I had the fortune of discovering and photographing transversely striated muscles in an insect (Nature, 1935, p. 761). The structures which I interpret as a rare case of completely fossilized muscles of a Palaeozoic arachnid are shown in Figure 30. One of these (PTR) is probably the protractor of the first right leg. The other two (MS) seem to belong either to the chelicerae or to the pedipalpi, but cannot be identified with certainty.

Circulatory System

The heart of Arachnida is a muscular tube situated in some species so close to the dorsal body wall that its pulsations may be observed through the latter. More often the thickness of the body wall and the somewhat greater distance between the latter and the heart make the heart invisible from the outside. In Palaeozoic Arachnida the heart has been observed and photographed only once, by myself, in a specimen of *Orthotarbus robustus* of Illinois. The beginning of three posterior arteries is also visible. It is a unique case and there is little chance of discovering another one like it.

Digestive System

The digestive system of Arachnida is well known and, in a general way, is built more or less on the same plan in all orders. It has never been used for taxonomic purposes, although, as we shall presently see, at least one feature of it, namely the position of the mouth and of the mouth parts engaged in food ingestion, is of the greatest importance. Within an order, the digestive system has been

studied fairly extensively only in spiders, much less so in Acari and scarcely at all in any of the other orders where its comparative anatomy still remains an untouched field.

The mouth is rarely visible from the outside even in alcoholic specimens of Recent species, being usually concealed from view by the adjoining appendages. Its original, ancestral position still present in the earliest stages of embryonic development, was at the anterior end of the body, just as the original position of the anus was at the posterior end. But, as it has been repeatedly shown by various investigators, the original position of the mouth never persists in the adult. During embryonic development the mouth slips backward, ventrally and posteriorly, so that the originally postoral first pair of appendages, the chelicerae, becomes preoral. There is no exception to this rule in Arachnida, but the final position of the mouth differs, sometimes, as in Opiliones, even in the same order. Where the mouth parts have not been greatly modified, the mouth is bordered anteriorly by the anterior lip (labrum) and posteriorly by the posterior lip (labium). It is unfortunate that the terms used for the designation of these structures in various orders of Arachnida are not always the same, causing not a little confusion, unless one is familiar with the particular terminology of each author. Thus the labrum is variously spoken of as the anterior or upper lip, rostrum, camarostome, taphrognath; the labium as the posterior or lower lip, or lophognath. In former years, the anterior lip was supposed to represent a somite with its own neuromere, but later researches, especially those of Hanström, have shown that this is not the case and that the anterior lip is an outgrowth of the body wall and receives its nerves from the so-called stomodeal bridge intimately connected with the chelicerai ganglia. The posterior lip may be either the sternite of the first pair of appendages, the chelicerae, as in Palpigradi where it is homologised with the prosternum; or it may be a functional modification of the second, pedipalpal sternite, as in spiders; or it may be altogether wanting as in some Opiliones. To avoid further confusion I shall use identical terms in all Orders of Arachnida.

The simplest and in some ways the most primitive condition in the structure of the mouth parts is found in spiders which in other respects present highly specialized features, and notwithstanding the fact that their posterior lip, as just mentioned, is a modified deuto- and not protosternum. Here the mouth is situated ventrally

between the pedipalpal coxae and may be closed or opened by the two lips. The lips themselves do not serve as strainers, but this function is taken over completely and very efficiently by the pharynx, the anterior plate of which is connected at its proximal end with the anterior lip, the posterior plate with the posterior lip. In scorpions the mouth is also ventral, but the entrance to it is anterior. The posterior lip is lacking and its place below the mouth is taken over by the four maxillary processes of the anterior two pairs of pedal coxae. The pharynx has no strainer, but the function of filtering the food is efficiently done by the brushes of the maxillary lobes. The mouth of the majority of Opiliones lacks a filtering apparatus, although it is provided with both an anterior and a posterior lip and with two or even three pairs of maxillary processes. In the Suborder Cyphophthalmi, as in the other Opiliones, the mouth opens ventrally. But unlike the condition in other Opiliones, it opens not directly to the outside, but into a cavity comparable to a bowl turned upside down. This depression was described first by Thorell who called it "stomotheca." A more detailed description of it is given below in the chapter on the Order Architarbi, to which the reader is referred. The formation of the stomotheca is due to a dorso-posterior displacement of the pedipalpal coxae, accompanied by a loss of the posterior lip. It represents an extreme development of the same type of mouth formation as the primitive one of spiders. A simpler modification of the primitive type is found in Phrynichida and Pseudoscorpiones.

A very different arrangement is found in Thelyphonida, Schizomida and probably in the extinct Order Kustarachnae. Pocock, who gave the first description of it, attempted to homologize the mouth parts of Thelyphonida with those of other Arachnida of the type which I call primitive. The anterior lip which he calls camarostome is most certainly the same in all Arachnida. But here the homology stops, for the rest of the mouth parts are unique in their structure and development. I shall call this type camarostome, restricting the use of the term to the kind of structure found in Thelyphonida and Schizomida and applying it to the entire apparatus and not to the anterior lip alone, as Pocock did. I would also like to call attention to the spelling of this term. Some authors use the letter *e* in place of an *a* and speak of a camerostome. This is an improper mixture of Greek with Latin and is objectionable.

The ventral surface of Thelyphonida and Schizomida presents no

opening leading to the mouth. Therein is the most important distinction between the stomotheca of the Cyphophthalmi and the camarostome. The stomotheca opens to the outside ventrally and the mouth opens into its roof. The camarostome opens dorsally and the access to it is anterior, between the pedipalpal coxae and the porrect chelicerae. The roof of the camarostome is formed by the fleshy anterior lip (Figure 52 LM), the floor—by a cup-like depression in the wall of the pedipalpal coxae. These coxae, as we have seen, are permanently fused with each other and although the line of fusion is visible from below, the cavity is a continuous and common one for both coxae. The upper (anterior) lip fits snugly into the cuplike depression and together they serve as a strainer, because their walls are covered with a thick brush of bristles. The true mouth is at the posterior end of the camarostome and leads into a pharynx. Figure 51 shows the camarostome in side view, as it appears when the lateral wall of the pedipalpal coxa has been removed on one side. Figure 50 shows a longitudinal microscopic section passing through the camarostome. A comparison of Figures 50 and 52 will show that the cavity of the camarostome opens to the outside by means of the narrow slit along its circumference when the upper lip is raised. A posterior lip is wanting. Its function is taken over by the floor of the camarostome.

In the Solifugae we meet with another structure. Here the mouth opens anteriorly, at the end of a "beak" formed by the fusion of the upper (anterior) lip with the lower (posterior) lip which is homologous to the deutosternum and is situated between the pedipalpal coxae.

The mouth of the Acari presents several modifications which are correlated with their life and type of food. The homology of their mouth parts is not always clear. Their discussion may be best left to specialists to whose work the interested reader may be referred for information.

But what about the position of the mouth and the structure of the mouth parts in extinct orders of Arachnida? Are they of the type found in now living Arachnida, or do they show structures which disappeared with their extinction? The arrangement of the coxae in *Eophrynus* and *Pleophrynus* (Figure 20) is so similar to that in Recent spiders that we can assume with a fair degree of probability that their chelicerae, their mouth parts and the position of their mouth were the same. This assumption finds support in

Hirst's description and figures of Devonian *Palaeocharinidae* closely related to the *Eophrynidae* (Figure 118). The structure and position of the chelicerae and pedipalpi in the Genus *Trigonotarbus* are shown in Figures 19, 104 and 105, and they, and those of *Anthracosiro* follow the araneid type.

In the Order Kustarachnae (Figure 15) the coxae are arranged radially around a minute sternum and the two pedipalpal coxae are fused together forming a single triangular plate without a trace of their paired origin. The general appearance of the Kustarachnae and the presence of a small pygidium at the end of their abdomen remind one of the Thelyphonida more than of any other order. The arrangement of the coxae is of course quite different and peculiar to themselves. But the fusion of the pedipalpal coxae is again a character similar to that in Thelyphonida. I think it is safe to assume that Kustarachnae had a camarostome comparable to that in Thelyphonida, hidden from view from below by the fused pedipalpal coxal plate. Naturally, there is also some resemblance to the Phrynichida (Figure 17) but the pedipalpal coxae in the latter are entirely free and independent of each other.

The Architarbi (Figure 12) have been often compared with the Opiliones and especially with the Suborder Cyphophthalmi (Figure 11). Usually only the four pairs of pedal coxae are visible in Architarbi. In some cases a pair of small wedge-like coxae are present between the ends of the first pedal coxae. I assumed in the past that in genera in which only four pairs of coxae are visible, the pedipalpal coxae are completely fused with the first pedal coxae. This explanation seems to me now quite erroneous for the following reason: the palpi in such specimens never show the expected number of segments. I think now that the correct interpretation is this: the first pedal coxae are movable and can be slightly separated in their anterior half, thus bringing into view from below the pedipalpal coxae which are otherwise concealed by the first pedal coxae. In other words the pedipalpal coxae are situated not in front of the first pedal coxae, where one would naturally expect them to be, but *dorsally* to them. The anterior processes of the first coxae are their own processes and not the remnants of pedipalpal coxae. Concealed above the first coxae is probably a stomotheca comparable to that in Cyphophthalmi with access to it through the slit between these coxae. A more detailed discussion of this subject will be found in the chapter on Architarbi.

The arrangement of the coxae in *Plesiosiro* (Haptopoda) and in *Anthracomarti* with five longitudinal rows of tergal plates, remained unknown until the present. Now, however, owing to a few extremely well preserved specimens in the collection of the British Museum, I am able to give a very clear picture of the coxo-sternal region in both these orders. When I first saw the thoracic ventral surface in a specimen of *Cryptomartus priesti*, I was greatly intrigued by the presence of an extra pair of coxae, wedged in between the pedipalpal coxae, making the total number of coxae grouped around the sternum six pairs and not five pairs as usual in Arachnida. The specimen in question bore evidence that the visible surface was the *inside* and not a mold of the outside surface of the coxae. In other words, looking at it under microscope one sees a picture comparable to that which one gets by looking at the ventral wall of the body-cavity of a Recent arachnid after removal of the dorsal wall and of all internal organs. An imperfect mold of the specimen could be seen on the reverse piece, and when this was cleared away, a perfect mold of the inside of the carapace appeared in its place. In the depth of the wedge-shaped coxae one could see four distinct openings shown in Figure 26 as black dots. Several other specimens presented the same picture. Two of these are shown photographically in Figures 208 and 209. Less perfectly preserved, but still recognizable they appear in Figure 222 in a specimen of *Cleptomartus plantus* and in Figure 235 in *Plesiosiro madeleyi*. For a long time I was quite unable to interpret the picture of the ventral surface in these fossils. There are no living Arachnida with a disposition of coxae of this type. I took the trouble of comparing these specimens with the coxo-sternal region of representatives of every Recent order both from the outside and from the inside. An added source of confusion was presented by the discovery of what I first interpreted as the basal joints of chelicerae, visible in several specimens and shown photographically in Figures 220-222 and 225, because of their striking resemblance to the basal joints of chelicerae in spiders. The chelicerae of *Palaeocharinoides* are well described by Hirst and resemble the chelicerae of *Liphistiis*, and up to the present *Palaeocharinoides* was considered to be a genus of *Anthracomarti*. But if the specimens of *Anthracomarti* which I studied had similar chelicerae, then their preserved segment would be the basal one. Both its ends show articulation points which would correspond respectively to the cephalothoracic articulation at the proximal end and to the

fang articulation at the distal end. But in that case the wedge-shaped coxae with the four holes would have to be regarded as a supernumerary pair, one in excess of the six pairs common to all Arachnida. On the other hand, if these coxae represented the basal joints of the chelicerae, then the segments shown in the figures would have to be the dislodged second joints of three-jointed chelicerae and the position of the coxae would be quite unlike that in any known arachnid. The second of the two alternatives seemed to be more probable. Chelicerata with supernumerary appendages are found only in the Class Pycnogonida which have too many peculiarities of structure to be considered in this connection. Further search for possible analogies lead me to an examination of the Xiphosura and of published figures of Eurypterida. The arrangement of the coxae in both these classes, while not quite the same as in *Cryptomartus* and *Plesiosiro*, is nevertheless strikingly similar (Figures 27 and 28 and photograph Figure 228). In the Eurypterida the chelicer basal joints are ventral in position, situated behind the doublure of the carapace and between the pedipalpal coxae. The mouth is also ventral in position and is situated between the chelicerae. In Xiphosura the chelicer basal joints are also situated behind the doublure, between the pedipalpal coxae (Figure 28), but the mouth, which is also ventral in position, is further back and is situated between the bases of the first pedal coxae. In *Plesiosiro* the mouth appears as a transverse opening between the chelicer basal coxae and the sternum at least in one specimen, and in *Cryptomartus* it may be seen in this position in two specimens. Of course, the coxae in both *Plesiosiro* and *Cryptomartus* are much closer together than in either the Eurypterida or the Xiphosura and their carapace has no doublure. But the similarity of the general plan is unmistakable.

Is this similarity in the disposition of the coxae sufficient to postulate closer relationship between these fossils and either the Xiphosura or the Eurypterida? I think this question may be answered decidedly in the negative. It is almost the only character in common with the Xiphosura. The Eurypterida have been often regarded as either the ancestors of the scorpions or at least as closely related to them. Personally I have always taken exception to these views and see no reason to change my opinion. Rather than to add to the resemblance between some Eurypterida and the scorpions, the disposition of the coxae and the position of the mouth alienates them from the latter. The proper answer seems to me to be that

we are in the presence of a similar evolutionary trend manifested independently by the two orders of Arachnida, by the Eurypterida and by the Xiphosura. We must not lose sight of the fact that the ventral position of the mouth and of the cheliceral coxae is not the original one. The shifting of the originally anteriorly situated mouth opening ventrad and backward was accompanied in Eurypterida and Xiphosura by the formation of the doublure. In the Eurypterida the mouth is *between* the chelicerae, i.e. nearer its normal position than in Xiphosura, although it is impossible to decide whether that is a primary condition or was achieved secondarily. In Xiphosura both the chelicerae and the pedipalpi lie *in front* of the mouth, and both receive their nerves from the ventral ganglionic mass. The Xiphosura are therefore in some respects more primitive than the Arachnida and in other respects more advanced. In *Plesiosiro* and *Cryptomartus* the position of the mouth also represents a step in advance of that in other Arachnida. The shape of the cephalothorax, the absence of a doublure and the consequent probable difference in the position of the brain and some other organs as compared with the Xiphosura make me think that the chelicerae in *Plesiosiro* and *Cryptomartus* received their nerves from the brain and not from the ventral ganglionic mass.

The question as to what the four holes in the cheliceral coxae do represent can be answered very definitely. The posterior pair leads into a pair of ventral thorns. The edge of these openings is rounded, smooth and more or less funnel-shaped. To settle the question definitely I chose specimen No. 13856 of *Cleptomartus plantus* and exposed the thorn to view, owing to a lucky presence of a cavity around it (Figure 86). The anterior pair of holes has a straight anterior edge, but is rounded behind. In at least two specimens there is evidence of an articulation membrane around the edge of the hole. The transversely straight anterior edge clearly marks the articulation axis between the cheliceral coxa and the second cheliceral joint. To be able to reach the mouth, the movable portion of the chelicerae must be considerably longer than the coxa. In *Plesiosiro* a complete, chelate chelicera is preserved. It is three-jointed, the process of the middle-joint serving as the immobile finger. Unfortunately in none of the specimens of *Anthracomarti* could I find the third joint. Since, however, the second joint never shows any process at its distal end, the probability is that the terminal joint was similar to a fang rather than a movable finger. Fritsch's

Figure 44 of *Anthracomartus minor* Kûsta is altogether fanciful and presumably wrong.

The digestive system itself has never been seen in any fossil Arachnida, probably because it disintegrated before it could become fossilized. Nevertheless I think that some specimens in the collection of the British Museum present evidence of a foregut extending to the end of the cephalothorax. At least one can see for example in specimens No. 22842, 31237 and 31268 of *Cryptomartus priesti* a shiny, trough-like depression extending from the proximal end of the cheliceral coxae to the end of the cephalothorax. At its posterior end this trough dips downward and becomes lost from view at the level where the abdomen begins. The depression corresponds closely to what one would expect to see of the endosternite with the oesophagus occupying its median line. The shiny, smooth surface of the trough makes it almost certain that it is not a casual modification of the matrix.

In all those fossil Arachnida in which the anus is closed by an operculum, the latter is usually well visible on both surfaces. It belongs, of course, to the ventral surface, but its inner surface is often better visible on the dorsal, than on the ventral surface. The appearance of the operculum is different in different orders. In *Anthracomartus* it is disc-like and clearly composed of two valves. The anterior valve is much larger than the posterior valve (Figures 68 and 92). In *Architarbi* it has the appearance of a single disc, though sometimes a median, short line is present in its anterior half, suggesting the existence of a right and left valve. In *Haptopoda* it is transversely ellipsoidal and apparently composed of a single valve. In *Trigonotarbi* it is disc-like and seemingly composed of a single valve. Pocock interpreted the anal operculum as a remnant of the last abdominal segment. While this may be so, it seems to be also possible that it is only a differentiation of the last sternite, comparable to the genital opercula of the second sternite.

Reproductive System

The diversity of structure is perhaps the most characteristic feature of the reproductive system in Arachnida. It is different in every order and presents considerable variations within the same order. In fossil Arachnida only the genital openings have been described and these in only a few cases. In the majority of Recent Arachnida the sex may be distinguished by secondary sexual characters such as

the proportions of the body and appendages, while in adult spiders the males are distinguished by the presence of the copulatory organs on the palpi and in adult Ricinulei on the third legs. Up to the present no indications of the sex had been discovered in any Palaeozoic Arachnida. It is probable that whenever the preabdomen of a fossil scorpion is so distended that the tergites are clearly outlined and their length and width is smaller than the length and width of the complete segment as represented by the pleura and intersegmental membrane, the specimen is a female. Yet disintegration of the inner organs and distension of the abdomen under pressure in the process of fossilization could result in a similar picture. The genital opercula of fossil scorpions, figured by Fritsch, Pocock and myself, closely resemble the opercula of Recent species. In Ricinulei I figured the genital opening in two fossil American species, and since the third legs of these specimens show no copulatory apparatus, the assumption is warranted that the specimens in question are mature females. A pair of disc-like openings were figured by me in several species of American Architarbi and possibly are seminal receptacles, but the sex cannot be determined with certainty. Pocock's figure of *Eophrynus prestvicii* shows the genital opening which resembles the atrium described by me later and figured in *Pleophrynus ensifer*, but again, the sex remains uncertain in both species.

The rich collection of fossil Arachnida of the British Museum contains several specimens of *Cryptomartus priesti*, one of *Cryptomartus hindi* and several of *Cleptomartus plautus* in which the genital region is exceptionally well preserved. All these specimens show three deep depressions, the first belonging to the second sternite and harboring in its depth the genital opening; the second belonging to the third sternite and presumably serving for the accommodation of some portion of the reproductive system; the third to the fourth sternite, having possibly to do with the mechanism of flexion of the abdomen along the intersegmental line between the fourth and fifth segments. This last impression, marked in my figures with a letter C, has approximately the same shape in all specimens, while the other two depressions, marked with the letters A and B, are dimorphic and yet present a parallel dimorphism in both *Cryptomartus priesti* and *Cleptomartus plautus*. The two species are well characterized by other structures, irrespective of this dimorphism. Therefore the difference in the appearance of the depressions A and B can be referred only to sex. But which sex is which? The sexual

organs themselves are not preserved. The relative proportions of the carapace and legs furnish insufficient data for distinction and at best would only confirm the existence of a difference; but without corroborative evidence they would not settle the problem as to *which proportions* are characteristic for this or that sex. After a long search for secondary sexual characters among representatives of Recent Arachnida belonging to all orders I finally found in *Mastigoproctus giganteus*, a whipscorpion common in Arizona, structural characters reminiscent of those in *Anthracomarti*. If one examines a male *Mastigoproctus* from below (Figure 43), one notices at once a triangular area marked in the figure with the letter B, distinctly raised above the surface of the third sternite. The apex of this triangle is directed backward and reaches the posterior edge of the sternite. The second sternite is smooth and uniform. Outlines of lungs are barely noticeable through the thick chitin. Looking at the same specimen from above after removal of the dorsal body wall and of all soft tissues (the latter by KOH) one obtains a view shown in Figure 45. Between the first pair of lungs in the second sternite the genital atrium (uterus masculinus externus of Börner) is plainly visible (ATR). On each side of the atrium is an apodeme for the attachment of the longitudinal muscles. Between the lungs of the second pair, situated in the third sternite, a pair of seminal vesicles (SV) are situated. They fit with the ventral portion of their body into the triangular depression which appears as the raised area B on the outside of the sternite. The opening of the atrium to the outside, i.e. the genital opening, is not readily visible in the majority of specimens, but when the abdomen is slightly distended, it becomes plainly visible from the outside at the posterior edge of the sternite between the two lung slits. It is shown considerably enlarged in Figure 49.

The ventral surface of a female *Mastigoproctus* presents a somewhat different picture from the male (Figure 44). Here the third sternite is of uniform level and the genital opening leading into the atrium (uterus externus femininus of Börner) is plainly visible between the second and third sternites. The surface of the second sternite presents a distinctly raised triangular area A which, unlike area B in the male, is directed with its apex forward. Figure 46 shows the inside view of the same specimen prepared in the same manner as the male shown in Figure 45. From this figure it is apparent that the raised area A which appears as a depression when viewed from the inside, serves for the accommodation of the female

genital atrium. The third segment in the female lacks chitinized structures except lungs and apodemes, and the soft organs found in the third segment evidently do not need additional space as in males. The triangular, externally raised areas (A in the female and B in the male) are always distinct in mature specimens and make the distinction of the sexes simple.

As already stated we find three depressions in all specimens of *Anthracomarti*. But when we examine the depressions more closely (Figures 47 and 48, *Cleptomartus plautus*), we notice a conspicuous difference in the shape of the depression A. It is long and narrow in specimen No. 18336, triangular in specimen No. 7916. Moreover, the apex of the triangle is directed forward in the latter. Examining the depression A of specimen No. 7916 at a slightly higher magnification and tilted at a slightly different angle, we are able to see in its central posterior lobe, which now appears as a clearly outlined bowl, separate from the confluent lateral portions of the depression, a pair of small, rounded depressions (SR) and in front of these a curved groove. The latter is certainly the genital opening and the pair of round depressions I interpret as the openings of seminal receptacles. The bowl is still better preserved in the type of this species, specimen No. 15896, shown in Figure 223 photographically, but the openings are not visible. Figure 71 shows the same region in *Cryptomartus hindi* and we are at once struck by the similarity of the structure which is the same in almost every detail, except for the shape of the genital opening which is perfectly straight. *Cryptomartus hindi* being much larger than *Cleptomartus plautus* described above, and the genital region of specimen No. 13955 being exceptionally well preserved, the photographic reproduction of the latter in Figure 198 is particularly enlightening.

Depression A in *Cryptomartus priesti*, specimen No. 15858 shown in Figure 73 shows more or less the same features. Unfortunately it is incomplete and not well preserved, while in specimen No. 31268 the posterior edge of the depression is bent forward so that the inside of the depression is barely visible.

Depression B shows also a slight, but appreciable difference in the two sexes. In the specimens which I consider to be females and which are shown in Figures 48, 71 and 73, the depression B is of the shape of a more or less wide pouch or a bulging pocket. In the specimens which I consider to be males and which are shown in Figures 47 and 72, the depression B is more strongly bent forward

and more like a cleft than a pocket. The function of these depressions is not clear. There are no openings in their walls. Presumably they were needed in both sexes for the accommodation of some portion of the reproductive system, perhaps seminal vesicles in males and seminal receptacles in females.

Sense Organs

It is an unfortunate fact that of the sense organs of Recent Arachnida only eyes, hairs and slit-organs are known. The last are presumably organs for the perception of odors or chemoreceptors in a wider sense, while sensory hairs of various types are for the perception of touch and of currents of air (trichobothria). While there can be no doubt that all Arachnida possess a sense of taste and many are probably capable of hearing sounds, no organs of hearing or taste are known with certainty.

The eyes in all Arachnida belong to the simple type. The number and disposition of eyes varies in all orders. In Ricinulei they are completely wanting, in other orders eyes may be wanting in some genera and present in other genera. The variations in internal structure are great and involve both the refractive apparatus and the retina. In the latter case these variations may be divided into two main groups, one in which the retina is direct and the other in which it is inverted.

Strange as it may seem, hairs in Palaeozoic Arachnida are very rarely preserved. Hirst has figured different types of hairs on the body and on the appendages of Devonian Arachnida, but it is well known that the preservation of fossils in the Old Red Sandstone is unusually fine. But even though Hirst's figures show four or five types of hair, it is impossible to decide whether any of them are strictly speaking sensory in function.

Eyes are often very well preserved. When the lens is fossilized as such, its inner surface is convex. When the specimen is merely a mold of the external surface, the eye appears either concave or flat, circular or elliptic in outline. Since similar modifications of the structure of the corneal lens are well known in Recent Arachnida, their presence in Palaeozoic Arachnida cannot be attributed to distortion during fossilization. On the contrary, it is evident that the lens presented already at this early period modifications which were directly related to greater or lesser perfection of vision. Some species were undoubtedly blind, but the absence of an impression of eyes

in a fossil arachnid is not always sufficient proof that the individual in question belonged to a blind species. Only eyes with a lens which is convex on its external surface are always well preserved and clearly visible in a fossil. An eye with a flat external surface may have been present, but left no impression on the matrix. Fortunately the inner surface is always convex. If such a lens is completely fossilized it may remain as such on the surface of the mold.

The fact that the eyes in some Scorpiones, Thelyphonida and Phrynichida resemble in their disposition Recent species speaks in favor of the assumption that Palaeozoic species already possessed eyes of both types, i.e. eyes with a direct retina and eyes with an inverted retina.

RELATIONSHIPS AND EVOLUTIONARY TRENDS

The new facts which came to light in the course of the present investigation are of such an unexpected nature that my own ideas concerning the relationships and evolutionary trends in Arachnida, expressed by me in my paper on Paleozoic Arachnida of Illinois and in the article "Arachnida" written for the new edition of the Encyclopaedia Britannica in 1945, have to be considerably modified. The segmentation of the abdomen in Haptopoda and Anthracomarti was not known for lack of necessary material. Errors of a serious nature crept into some of the older descriptions, partly because of insufficient preparation of the specimens, partly because of interpretations based on wrong theoretical considerations. The laws governing the disappearance of abdominal somites were not understood. The fusion of tergites and of sternites escaped consideration. The position of the mouth was not accounted for and assumed to be the same in all Arachnida. These are the reasons why, with new evidence at hand, I am now forced to erect the new Order Trigonotarbi for those genera of the old Order Anthracomarti, which are externally recognizable by the absence of submarginal abdominal tergal plates; to restrict the Order Anthracomarti to genera which have both marginal and submarginal tergal plates, and to unite the Anthracomarti, as delimited here, with the Haptopoda in one Subclass Stethostomata, new, because of the peculiarity in the arrangement of their coxae and in the position of their mouth. The study of the first tergite in Anthracomarti, Trigonotarbi and Recent Thelyphonida threw new light on the true segmentation of Silurian scorpions and the Pennsylvanian Genus *Mazonia* and induced the erection of a new suborder of scorpions, the

Protoscorpiones, for them, as opposed to the Suborder Euscorpiones including all other scorpions. A careful examination of the camarostome in Thelyphonida and of the stomotheca in Cyphophthalmi among the Opiliones and a comparison of the arrangement of their coxae with that in Architarbi and Kustarachnae lead to a new interpretation of the picture presented by these two extinct orders and explained features previously misunderstood and misinterpreted. The evolutionary trends within individual orders will be discussed in their own place. Here only the relationships of the different orders to each other and the trends which caused their evolution will be submitted for consideration.

Surveying the entire Class Arachnida we notice at once that modifications of the original segmentation occur both in the cephalothorax and in the abdomen and that these modifications are independent of one another. Thus a segmented carapace is characteristic of the Orders Palpigradi, Schizomida and Solifugae, but the abdomen of Palpigradi consists of eleven segments, the twelfth having disappeared; in Schizomida of twelve segments, the last three of which form a pygidium, and in the Solifugae of eleven as in Palpigradi, but the first abdominal segment is reduced to a petiolus to a greater extent than in the Palpigradi and a telson is wanting. Similarly in the other orders, all of which are characterized by an entire carapace, we observe similarities of structure in the cephalothorax in orders which are quite dissimilar in the structure of their abdomen. Thus the pedipalpi and first pair of legs in Thelyphonida and Phrynichida are so similar in these two orders and so different from the corresponding appendages of the other orders that the Thelyphonida and Phrynichida were considered to be closely related to each other and were placed until recently in a single Order Pedipalpi. Yet their abdomen presents many important differences of structure. The first fundamental law governing modifications of somatic characters in Arachnida may be therefore formulated as *independency of prosomatic and opisthosomatic evolutionary trends*. These trends include both external and internal characters, but in view of the fact that the internal anatomy of Palaeozoic Arachnida is not known, we shall limit our discussion here to external features visible in them.

Prosomatic Evolutionary Trends

We have already mentioned the segmentation of the carapace in three orders of Arachnida, the Palpigradi, the Schizomida and the

Solifugae. In all these orders the anterior plate or propeltidium is single and large, while the mesopeltidium and metapeltidium are paired and relatively small. Since the cephalothorax consists assumedly of not less than seven and possibly of more than seven somites, it is evident that the propeltidium represents the fusion of several anterior segments. We may say, therefore, that the trend of fusion of the thoracic tergites is in a direction from the front to the rear of the prosoma. Whether the same rule applies to cephalic tergites is impossible to decide, because no Arachnida with a fully segmented carapace are known. Evidences of segmental origin are preserved even in many species with a completely fused carapace, but the cephalic portion of it is invariably single. Nor is it possible to decide whether the cucullus of the Ricinulei is a remnant of original segmentation or a new acquisition correlated with its function as a movable, protective plate for the mouth. It is present in all Palaeozoic Ricinulei. The high specialization of this order in other respects makes it however probable that we have in the cucullus an early, new acquisition and not a remnant of an old character. The portion of the carapace in Pseudoscorpiones, lying in front of the eyes, is also called a "cucullus," but as Chamberlin points out (1931, p. 49) "should not be confused with the cucullus of the Ricinulei, in which group it is a movable, transverse, preocular plate and not necessarily (although probably) homologous with the cucullus of the Chelonethida." Chamberlin does not state why in his opinion this homology is probable.

The presence of a doublure in the carapace is characteristic of all Xiphosura and Eurypterida. In Arachnida a doublure is present only in Thelyphonida and represents a new trend which for some reason did not involve other important changes, for whereas in Xiphosura and Eurypterida it is correlated with a backward shifting of the mouth, in Thelyphonida the mouth has not been appreciably shifted, while in Haptopoda and Anthracomarti the mouth is considerably displaced backward, but the carapace is lacking a doublure.

The backward shifting of the mouth in the course of development is a fact well known. In all adult Arachnida the mouth is always posterior to the chelicerae from which it is separated by a more or less considerable portion of the ventral body wall and the upper lip. But the actual position of the mouth varies considerably in different orders and is correlated with the disposition of the coxae and the manner of feeding. Since the backward displacement of the mouth

is a departure from its original anterior position, the greater the displacement the more advanced in this respect the arachnid Order must be regarded. The end of this evolutionary trend has been reached by the Xiphosura. In this class of Chelicerata the mouth is actually situated between the coxae of the first pair of legs. Nevertheless not only the nerves of the pedipalpi, but also those of the chelicerae have their roots in the ventral ganglionic mass. In Haptopoda and in Anthracomarti the mouth is also situated between the first pedal coxae. In this respect they manifest a trend similar to that in Xiphosura although in all other respects they are typical Arachnida. In Thelyphonida, Schizomida and Kustarachnae the coxae of the pedipalpi are completely fused, and the mouth is hidden from view by their common ventral wall, above which a camarostome has developed. Perhaps somewhat different from this modification, yet more or less in the same direction as a trend, is the displacement of the pedipalpal coxae in Architarbi, in which they are situated dorsal to the contiguous coxae of the first pair of legs and are therefore usually concealed from view by the latter. Here the position of the mouth is not known. It is certain that the mouth does not open on the ventral surface of the body as in Xiphosura and Stethostomata, and the surmise is that a stomotheca resembling that in Cyphophthalmi is situated *above* the first coxae, although morphologically it is *anterior* to them.

The last external character of a higher than familial value is furnished by the thoracic sternal plates including the lower lip, which represents the anterior plate. In Palpigradi, Schizomida and Thelyphonida the sternal plates are still several in number and independent of each other, except in the case of the large plate following upon the lower lip, and apparently composed of two sternites permanently fused together. The fusion and disappearance of thoracic sternites in Arachnida is definitely correlated with the disposition of the coxae. It is clearly independent of the fusion of the corresponding tergites. An interesting feature is presented by the last thoracic sternite, the so-called metasternum, which, whenever present, is situated between the coxae of the fourth pair of legs (Figures 13, 14, 16, 18). But the same position is occupied by the first abdominal sternite in Arachnida which have completely lost the metasternum (Figure 24, Solifugae) and those in which the metasternum is reduced to a minute rudiment (Figure 18, *Liphistius* among the Araneae). The student of fossil Arachnida must be therefore extremely careful in interpreting the

triangular area enclosed between the fourth coxae, because this area, originally belonging to the prosoma, shows not only a trend toward complete disappearance, but also a later trend towards its invasion by the first abdominal somite. In the external anatomy of Arachnida this is *the only trend of the prosoma correlated with a trend of the opisthosoma*.

One usually pictures the juncture between the cephalothorax and abdomen (prosoma and opisthosoma) in some imaginary ancestor of Arachnida as occupying the full width of the body and having a more or less transversely ellipsoidal shape. This picture disregards the existence of the appendages and their specialization. No Arachnida with that type of juncture have ever existed, for already in the Silurian scorpions—the oldest known Arachnida—the juncture resembles that of Recent ones and departs considerably in many respects from this theoretical concept. The so-called “broad” juncture really refers only to the dorsal line of connection. On account of the displacement of coxae and of the correlated occupation by the anterior ventral abdominal wall of the vacated space between the fourth coxae, the ventral line of juncture is usually triangular and the field of juncture enclosed between the dorsal and ventral lines is rather of a complex shape as can be seen in scorpions when one severs the abdomen from the cephalothorax without rupturing the diaphragm separating them. On the other hand, in extreme cases of a petiolated abdomen, such as is represented by the spiders, the juncture is actually either transversely elliptic or else disc-shaped. This is due to the fact that in such cases the forward shifting of the coxae is practically negligible and the departure from the original, theoretical type of juncture left out the cephalothorax completely and involved only the anterior portion of the abdomen. Further changes in the abdomen had to follow different paths in the two cases and their evolutionary trends will be discussed separately. But the present study of Trigonotarbi has disclosed the fact that we have in them a group of Arachnida with more or less transitional stages of juncture. Of course, a certain number of transitional stages, from such in which the lateral edge of the carapace forms with the sides of the abdomen a convex or straight line, to such in which this line becomes concave and finally reaches the shape of a hairpin, is to be expected and actually exists. Thus in the Architarbi which are indisputably Arachnida with a broad juncture between the abdomen and the cephalothorax, the line forming the edge of the body is convex in *Architarbus*,

straight in *Opiliotarbus* and distinctly indented in *Metatarbus*. But the evolutionary trends exhibited by the abdomen of the Architarbi remain of the type found in Arachnida with a broadly joined abdomen and not in those with a petiolus.

Opisthosomatic Evolutionary Trends

The modification which involves the most serious consequences and leads to diverse evolutionary trends is the one which affects the volume of the first abdominal somite. The volume of this somite may be reduced by shortening of its length leading to its eventual complete disappearance, or by constriction of its periphery until its length becomes greater than its diameter and it assumes the shape of a pedicel. The former case is typical of Arachnida with broadly joined abdomen. In scorpions of the Suborder Protoscorpiones the first abdominal tergite still existed, but in those of the Suborder Euscorpiones it has been entirely lost except for its neuromere. In Pseudoscorpiones the first tergite is always well developed, but the sternite does not exist any more and in its place there is merely a soft connecting membrane. In Opiliones even the last traces of the first sternite have disappeared, but the tergite is incorporated in the dorsal shield. In Acari all traces of abdominal segmentation are lost. The first neuromere persists in all cases. Discrepancy between the number of tergites and sternites is due to fusions. In the Architarbi from four to six anterior tergites show the tendency to considerable abbreviation coupled with a forward displacement of the first and second sternites and sometimes followed by a fusion of some of the following sternites.

In the Stethostomata which have also a broad juncture between the cephalothorax and the abdomen, the first abdominal segment is comparable to that in Architarbi, but the tergite is only a little abbreviated and the sternite, although triangular, is of considerable size. In all Anthracomarti the second and third tergites are permanently fused. At the posterior end of the abdomen in all these orders a tendency towards a disappearance of segments is noticeable and exhibits the same principle of shortening, except in scorpions in which the diminution is due to peripheral constriction and not a single posterior segment has ever been lost, although a forward displacement of neuromeres takes place in all Recent scorpions and the last neuromere is fused with the penultimate one.

The first abdominal somite is never completely lost in orders

with a petiolated abdomen. The first abdominal segment of *Palpigradi* may be regarded as the most primitive form of pedicel. It has the shape of a short cylinder, distinctly more slender than the cephalothorax and about three times more slender than the abdomen, but not yet of the appearance of the pedicel in spiders. Because of a difference in the position of the fourth coxae and of the metasternum in *Thelyphonida* and *Schizomida*, as compared with *Palpigradi*, the first abdominal segment in these orders shows a distinct tendency to the disappearance of the first sternite, while the first tergite in *Thelyphonida* is normally overlapped by the carapace in the same manner as in *Anthracomarti* and *Haptopoda*. This process of overlapping without fusion or disappearance of the corresponding segment reaches its climax in *Ricinulei*. Here the first tergite exposed to view in the normal position of the animal is in reality the tergite of the third segment, that of the second being very short and concealed under the carapace, while the first tergite is quite small, forming the roof of the pedicel. The first sternite has completely disappeared. In *Ricinulei* as well as in *Thelyphonida* and *Schizomida* the last three segments of the abdomen show the tendency to disappearance by peripheral constriction, but they are not the same segments, for the pygidium of the *Thelyphonida* is formed by the 10th, 11th and 12th segments, that of the *Schizomida* by the 9th, 10th and 11th segments and the one of the *Ricinulei* by the 7th, 8th and 9th segments according to Hansen and Sørensen. Millot in his paper on the constitution of the abdomen in *Ricinulei*, published in 1945, maintains that the first abdominal somite has altogether disappeared as in scorpions, that the total number of abdominal somites in *Ricinulei* is 10 and not 9 and that the pygidium is, therefore, formed by the 8th, 9th and 10th segments. At any rate the pygidium of the three orders in question is not a homologous structure, but merely exhibits the same trend, a trend different from that in *Arachnida* with broad juncture of the abdomen, in which the posterior segments disappear without forming a pygidium. The last stage in the formation of a pygidium may be seen in the so-called anal tubercle of spiders. This tubercle is composed of from one to three segments representing the tergites of the last abdominal segments, the sternites of which have completely disappeared. But in spiders other than *Liphistiomorphae* the abdomen is reduced to five segments and the remnant represented by the anal tubercle corresponds therefore to the 6th to 8th segments.

Now in the order Trigonotarbi, newly established here, there are considerable differences in the manner of juncture between the abdomen and the cephalothorax. In *Trigonotarb* it is the full width of the body and the lateral edge is almost perfectly convex. The shape of the carapace in *Anthracosiro* is such that it is considerably wider in its middle than at its posterior edge. But the latter is straight and as wide as the anterior edge of the abdomen and is connected with the latter along its entire width. The first sternite occupies the same position in both genera, but the first tergite has apparently disappeared in *Anthracosiro*, while it is quite normal in *Trigonotarb*. The abdomen of *Anthracosiro* is composed of 10 segments, that of *Trigonotarb* only of 8 and the manner of disappearance of posterior segments is more or less of the type found in Arachnida with broad juncture of the abdomen. However, this juncture in *Pleophrynus* reminds one more of the juncture in Thelyphonida and the arrangement of the coxae and the presence of a single sternal plate is strongly reminiscent of what we find in Araneae. Perhaps the presence of both trends in the same organism resulted in the production of detrimental characters and is partly responsible for the extinction of this order.

Subsegmentation of Abdominal Somites

This phenomenon is a regular feature in scorpions, but in its initial stage may be observed in Trigonotarbi. In scorpions it is the eighth abdominal embryonic segment which subdivides and thus restores the normal number of 12 segments reduced to 11 by the disappearance of the first somite in the course of embryonic development. This subsegmentation which seems to be proven beyond any doubt, must have preceded the disappearance of the first somite, for the latter persists in the Silurian scorpions whose postabdomen shows all five segments as in Recent scorpions. In *Pleophrynus* and *Eophrynus* among the Trigonotarbi the first tergite shows evidence of subsegmentation in the shape of a faint transverse line. As I have shown (101) this line is the result of subsegmentation and not of fusion of two originally independent tergites, because the two portions together correspond to the first sternite, and there is no possibility for the existence of an evanescent sternite preceding the first, because the genital opening is clearly visible and is situated on the second sternite, i.e. in the position typical for the class.

Evolutionary Trends of Prosomatic Appendages

Most of the modifications found in prosomatic appendages are of lower than ordinal value. However, a few possess that value, for they are characteristic of an entire order. Such modifications are found in the pedipalpi which develop tactile functions in Solifugae and raptorial ones in Thelyphonida and Phrynichida. The most remarkable modification is, of course, the formation of the copulatory apparatus in male spiders. Its earliest known appearance is in the fossils of the Coenozoic and it is a pity that nothing is known of this important modification either from the Mesozoic or from the Palaeozoic.

The first pair of legs shows a modification into a tactile organ in Thelyphonida and in Phrynichida in which this trend reaches its greatest development.

The third legs are modified in Ricinulei as male copulatory organs, but how this modification came to be developed we have no idea, because no fossil Ricinulei have so far been found, which would permit the recognition of their sex.

The loss of some prosomatic appendages is of very restricted occurrence. In Acari the last two pairs of legs are wanting in the Tetrapodili, and are replaced by bristles in some other parasitic mites. In the development of Acari and Ricinulei the larval stage is characterized by the presence of only three pairs of legs, but this circumstance must not be confused with any trend to lose the fourth pair, since the latter is present in all later stages.

Evolutionary Trends in Opisthosomatic Appendages

Here, as in prosomatic appendages, most of the changes are of a lower than ordinal grade. To the latter may be referred only such cases in which modified abdominal appendages are retained in the adult, namely the combs of scorpions and the spinnerets of spiders. The combs are modified appendages of the third abdominal embryonic somite, the spinnerets of the fourth and fifth. Whether such structures as the "penis" of Phrynichida are modified appendages is not definitely established for lack of embryological evidence. The only evolutionary trend, then, of opisthosomatic appendages in Arachnida is their tendency to disappear and this tendency remains noticeable even in the case of the spinnerets the number of which is subject to diminution in a series of Recent species.

Evolutionary Trends of Internal Organs

Since evolutionary trends of internal organs cannot be studied in fossil Arachnida except to a very limited extent, it is not necessary here to consider them in detail. Only the briefest reference will be made to each system inasmuch as we know the trends in Recent Arachnida, with the purpose that the subject should not escape the notice of future investigators if more fossil material should become available.

The *muscular system* of the abdomen, consisting of longitudinal dorsal and ventral bands, of dorso-ventral paired muscles and of special muscles of the respiratory organs and of the abdominal appendages, naturally is involved in the same trend of segmental loss as the entire abdomen. In fossils one can see the attachments of the dorso-ventral muscles and under circumstances the apodemes for the attachment of pulmonary muscles.

The *book-lungs* show in Recent Arachnida a trend to gradual complete disappearance. There are four pairs of book lungs in scorpions, three pairs in Anthracomarti, two pairs in several orders, a single pair in the majority of spiders and only tracheal tubes in a few other spiders and in several other orders. Spiders of the Suborder Dipneumonomorphae are unique in having both book-lungs and tracheal tubes in the same individual. Only in Acari many species have no respiratory organs, respiration being accomplished by the alimentary system and the skin. Only in Palpigradi, Phrynichida and Architarbi ventral sacs are present. Tracheal tubes have never been seen in fossils, not because they did not exist, but undoubtedly because they become invisible in the process of fossilization. So far in fossil Arachnida book-lungs have been described only in Anthracomarti, Trigonotarbi and Haptopoda, ventral sacs in Architarbi.

The originally segmental *heart* shows a trend to lose posterior cardiomerites, but has been more or less extensively studied only in spiders. Whether the presence of two pairs of ostia in the cephalothorax of Thelyphonida and Solifugae is an ancestral character or a new acquisition, is not known at present, although a similar condition in Xiphosura speaks in favor of the first assumption and involves the existence of a trend different from that observed in the abdominal portion of the heart. In fossil Arachnida the heart was seen only in one specimen, namely in *Orthotarbus robustus* Petrunkevitch, No. 14878 of the Illinois State Museum.

The *coxal glands*, originally of presumably segmental nature,

exhibit a trend to lose outlets. No coxal glands have been seen in fossil Arachnida, while the outlets are never visible without special preparation even in Recent ones.

Many modifications of the *digestive system* in Recent Arachnida are known, but none have been studied sufficiently to indicate evolutionary trends. The digestive tract has as yet not been seen in fossil species.

The chief trend in the *nervous system* is the forward movement of abdominal neuromeres. This trend is found also in other Arthropoda and results in a greater or lesser concentration of the nervous system in the cephalothorax in Crustacea, Hexapoda and Arachnida. It is a trend of the greatest importance, for it reaches its climax in the highest representatives of each class. Since the nervous system is never visible in fossil Arachnida we can only assume that in the orders which survived up to the present time the nervous system of extinct forms exhibited already the same characteristic structure.

Of the *reproductive system* in fossil Arachnida we know absolutely nothing, except for the external openings in a few specimens. It seems strange that no impression of uterine eggs should have been left in the abdomen of a fossil arachnid, but I have never seen even the slightest indication of one.

Relationship between the Arachnida, Eurypterida and Xiphosura

There was a time when these three Classes were grouped together as Arachnida, and the Eurypterida and Xiphosura given the rank of orders equivalent to the orders into which Arachnida are usually divided. The idea that scorpions evolved from Eurypterida persisted until recently. We have already mentioned that Pocock, in his paper on the Scottish Silurian scorpion objected to Thorell's and Lindström's assumption that *Palaeophonus* was an air-breathing Arachnid and considered it to be an aquatic arthropod leading a life comparable to that of Recent crabs. I think it is safe to maintain now that *Palaeophonus* was an air-breathing scorpion, in other words, that all known now living as well as fossil scorpions are distinguished from the Eurypterida by the possession of book-lungs as against book-gills of the latter. Rather than to derive scorpions from already highly specialized Eurypterida, it is more reasonable to assume that both developed from an older arthropod stock. Both the Eurypterida and the Xiphosura possess many characters not present in any

arachnid and some of these characters are of fundamental value. The present discovery that the Haptopoda and the Anthracomarti have a disposition of the coxae, similar to that in Eurypterida and Xiphosura does not necessitate a return to the old idea of their relationship. It merely shows that the evolutionary trend of backward displacement of the mouth has reached its climax in two extinct orders of Arachnida, as it has in Eurypterida and Xiphosura. It seems to be a general trend of all Arthropoda and the fact that it reached its climax in three different classes merely indicates the probability of the existence in all three cases of similar morphogenetic factors.

PHOTOGRAPHY

Photography of fossil Arachnida is not as simple as it appears to be at first glance. The usual method of making the specimen white by spraying it with an atomized solution of ammonium chloride is unsatisfactory from several points of view. It obliterates the difference in color between the specimen and the matrix and makes finer structures less visible. It renders some structures completely invisible by changing their edge sufficiently to affect appreciably the angle of reflection. It is very difficult to give a really uniform coating to deeply concave surfaces of small dimensions. It does not improve the picture, and the gain in time due to shorter exposure is upset by the loss of time required for spraying. The recently proposed method of using magnesium oxide (Rasetti, 1947) instead of ammonium chloride is no better in this respect and the former has the additional disadvantage of being insoluble in water and therefore more difficult to remove after its use. Extensive experience has convinced me that the best results are obtained when the specimen and the matrix are left in their natural state and only the illumination is varied. The latter has to be powerful, because most specimens have to be photographed at magnifications requiring a diaphragm aperture of f.16 or f.22 to get different levels in sharp focus. The optical equipment used in this work consisted of microtessars and only in the case of the eyes of scorpions shown at a much higher magnification than can be obtained with the microtessars, a microscope with a 16 mm. apochromat and a compensating ocular was used. For illumination two, and in some instances three, ribbon filament lamps with condensers were used. The approximate angles of illumination for best results were first determined by examining the specimen under a binocular microscope. Then the

same lamps were placed in approximately the same position around the camera and the image examined on the ground glass. Usually it was necessary to shift slightly the position of each lamp and properly adjust the angle of incidence. Often the intensity of the light of the one or the other lamp had to be changed by moving the condenser. Whenever possible, a ground glass was used in front of each lamp to get greater diffusion. Orthochromatic or panchromatic plates were used. When it was desirable to lessen the contrast the exposure was purposely prolonged up to twice or three times the normal one and potassium bromide added to the developer. No ray filters of any kind were used.

CLASSIFICATION

Key to orders of Arachnida, based on external characters visible in fossils.

1. Dorsal surface 2
- Ventral surface 18
2. No constriction, or only a slight constriction between the carapace and the visible anterior end of the abdomen 3
- Constriction between carapace and abdomen very distinct ... 11
3. A movable plate or cucullus present in front of the carapace, separated from the latter by a distinct transverse line. The line between the carapace and the abdomen always straight. The anterior edge of the abdomen is formed by the edge of the third tergite and the juncture between the abdomen and the cephalothorax is of the petiolate and not of the broad type, although it has that appearance in both Recent and fossil species. The abdomen presents four tergites to view, followed by a small pygidium composed of three annular segments, which are extrovert in fossils, but telescoped in Recent species. In the fossil Genus *Curculioides* the four abdominal tergites visible in other Ricinulei are fused into a single shield with a slightly curved longitudinal line dividing it into a right and left field. (Carboniferous and Recent.) Order *Ricinulei*.
- Carapace without a cucullus. Abdomen of variable shape, but never ending in a pygidium 4
4. Abdomen always subdivided into a preabdomen and a post-abdomen or tail. The preabdomen is as wide or wider than

the carapace and is composed of seven or eight segments. The postabdomen is always composed of five segments and has at its end a poison-gland with a sting. The postabdomen is always much more slender than the preabdomen. (Silurian, Carboniferous, Triassic, Tertiary and Recent.) Order *Scorpiones*.

- Abdomen not subdivided as in scorpions, nor does it end in a poison-gland 5
- 5. Abdomen broadly rounded behind, sometimes festooned and always clearly divided into five longitudinal rows of tergites. If the appearance suggests the existence of seven instead of five rows, the extra two longitudinal lines responsible for this belong to the ventral surface of the abdomen and are merely superimposed on the dorsal surface. (Carboniferous and Permian.) Order *Anthracomarti*.
- Abdominal tergites either entire or else forming not more than three longitudinal rows, or fused with carapace 6
- 6. Abdominal tergites divided into three longitudinal rows, the plates forming the central row usually much wider than the corresponding marginal plates. Carapace triangular and high, or transversely elliptic and flat. (Devonian and Carboniferous.) Order *Trigonotarbi*.
- Abdominal tergites either entire, or divided by a median longitudinal line, or fused with the carapace 7
- 7. Tergites fused with the carapace without a trace of intersegmental lines. (Devonian, Cretaceous, Tertiary and Recent.) Order *Acari*.
- Intersegmental lines clearly visible 8
- 8. From four to six anterior tergites greatly abbreviated and divided by a fine, median line. (Carboniferous.) Order *Architarbi*.
- Anterior tergites not conspicuously abbreviated, or only the first tergite abbreviated and often concealed from view by the overlapping posterior end of the carapace 9
- 9. Carapace low, pointed anteriorly, with a median and a pair of lateral ridges. A pair of round eyes near anterior end. Intersegmental lines straight. Abdomen composed of eleven segments. The second tergite is the longest, the first ter-

gite is greatly abbreviated and either concealed under the carapace or fully exposed. Palpi pediform, short and slender. All legs with segmented tarsi. (Carboniferous.) Order *Haptopoda*.

- Combination of characters different from the above 10
- 10. Pedipalpi never chelate and always shorter than the legs which are often very long and thin. Carapace and abdomen of fossil species furnish no tangible characters for differentiation of harvestmen from pseudoscorpions, with which they have otherwise very little in common. (Carboniferous, Jurassic, Tertiary and Recent.) Order *Opiliones*.
 - Pedipalpi always longer than the legs, powerful, chelate, resembling those of scorpions from which the pseudoscorpions are easily distinguished by the shape of their abdomen. Abdominal tergites either entire or divided in two. (Tertiary and Recent.) Order *Pseudoscorpiones*.
- 11. Carapace segmented. If its segmentation is not visible externally, then the abdomen ends in a pygidium. If the pygidium bears a multi-segmented whip or flagellum, the palpi are slender, not raptorial. If the whip is composed of not more than three segments, then the femora of the fourth pair of legs are distended 12
 - Carapace entire, composed of a single sclerite 14
- 12. Abdomen without a pygidium. Carapace clearly segmented. Chelicerae two-jointed, chelate, stout, as big as the carapace. (Carboniferous and Recent.) Order *Solifugae*.
 - Abdomen with a pygidium 13
- 13. Abdomen with a multi-jointed whip. Pedipalpi pediform. (Jurassic and Recent.) Order *Palpigradi*.
 - Whip one- to three-jointed. Pedipalpi raptorial. Fourth femora distended. (Tertiary and Recent.) Order *Schizomida*.
- 14. Abdominal tergites divided into three longitudinal rows, sometimes with conspicuous tubercles and with two pairs of posterior spines. Carapace triangular, with a pair of eyes; its posterior edge straight and as wide as the anterior edge of the abdomen, but joined to the latter only by its middle third. (Devonian and Carboniferous.) Order *Trigonotarbi*.
 - Abdominal tergites entire or segmentation obscured 15

15. Abdomen without a pygidium, but with an anal tubercle situated above the anus and composed of from one to three segments (not visible in fossils). The abdomen may be segmented or segmentation may be restricted to posterior end, or completely lost. The full number of abdominal segments is never visible in fossils and cannot be seen in Recent species without rotating the specimen. Lateral soft pleurae wanting. Pedipalpi pediform. (Devonian, Carboniferous, Permian, Tertiary and Recent.) Order *Araneae*.
 - Abdomen with a distinct pygidium. Pedipalpi powerful, raptorial (or not known) 16
16. Pedipalpi not known. Chelicerae three-jointed, chelate. Legs long and thin. Carapace wider than long, with a pair of eyes. Abdomen more or less cone-shaped, pointed behind, with a pygidium, but without a whip, segmented, with soft pleurae. (Carboniferous.) Order *Kustarachnae*.
 - Pedipalpi powerful, raptorial. First pair of legs modified as tactile organs with segmented tarsus 17
17. Carapace distinctly longer than wide. Abdomen with a segmented whip. Pygidium three-jointed. (Carboniferous, Tertiary and Recent.) Order *Thelyphonida*.
 - Carapace wider than long. Abdomen without a whip. Pygidium single-jointed. If the appendages are missing, the fossil may be mistaken for a spider, but can be identified by the presence of usually well visible lateral pleurae. (Carboniferous and Recent.) Order *Phrynichida*.
18. Abdomen subdivided into a preabdomen which is as wide as the carapace, and a postabdomen or tail, which is much more slender and ends in a poison gland with a sting. Behind the genital opercula a pair of combs is present. Pedipalpi powerful, chelate, more prominent than the legs. (Silurian, Carboniferous, Triassic, Tertiary and Recent.) Order *Scorpiones*.
 - Abdomen not subdivided. Combs wanting 19
19. Pedipalpi powerful, longer and stouter than the legs, chelate. Chelicerae two-jointed, chelate. All coxae contiguous or nearly so. Abdomen with twelve sternites, but the first and the twelfth rudimentary. In some species the sternites may be

- divided by a median, longitudinal line. (Tertiary and Recent.) Order *Pseudoscorpiones*.
- Palpi not as above 20
20. All six pairs of coxae in the same plane, arranged in two rows converging at both ends. Anterior two pairs contiguous and the cheliceral coxae flanked by the pedipalpal coxae. The cheliceral coxae are in contact with each other along their entire mesial edge and each possesses two foramina, one behind the other, the four forming together a rectangle. The mouth is situated behind the anterior four coxae and appears as a transverse slit between the first pedal coxae. A narrow and long sternum is situated behind the mouth 21
- The cheliceral coxae lie in a different plane from the other coxae, so that only five pairs of coxae are visible. The pedipalpal coxae may be fused into a single, triangular plate, or they may be concealed by the coxae of the first pair of legs. In that case the pedipalpal coxae lie in a higher plane than the pedal coxae, with the result that only four pairs of coxae are visible 22
21. Abdomen with ten sternites, of which all but the first and the last have marginal fields, clearly separated by a pair of longitudinal lines from the median fields. The field behind the tenth sternite is the ventral portion of the tenth tergite. A more or less circular anal operculum is situated on the tenth sternite. (Carboniferous and Permian.) Order *Anthracomarti*.
- Abdomen with eleven sternites, of which the third to ninth are divided by a longitudinal, median line. Marginal fields wanting. Anal operculum on the eleventh sternite. Second sternite very large, with a strongly convex, procurved posterior edge. Tarsi of all legs segmented. Chelicerae three-jointed, chelate. (Carboniferous.) Order *Haptopoda*.
22. Abdomen with a pygidium 23
- Abdomen without a pygidium 28
23. Pedipalpal coxae widely separated. Abdomen with eleven sternites, ending in a segmented whip. Pedipalpi pediform. (Jurassic and Recent.) Order *Palpigradi*.
- Pedipalpal coxae approximated, contiguous or fused 24

24. In front of the chelicerae a transverse plate is situated—the ventral portion of the cucullus. All tarsi segmented. Pygidium composed of three annular segments, extrovert in fossils, telescoped in Recent species. No whip. (Carboniferous and Recent.) Order *Ricinulei*.
 — Cucullus wanting 25
25. Coxae arranged in successive pairs, forming two more or less parallel rows 26
 — Coxae radiating from a central sternum 27
26. Pedipalpi powerful, very stout, raptorial. First pair of legs modified as tactile organs with segmented tarsus, their coxae much more slender than those of the succeeding pairs. Fourth femora normal. Abdomen ending in a long, multi-segmented whip. (Carboniferous, Tertiary and Recent.) Order *Thelyphonida*.
 — Pedipalpi not conspicuously stouter than the legs. First pair of legs not modified, their coxae cylindrical, as stout as and longer than those of the third pair. Fourth femora distended. Abdomen with a whip composed at most of three segments. (Tertiary and Recent.) Order *Schizomida*.
27. Pedipalpi powerful, very stout, raptorial. First pair of legs modified as tactile organs. Their metatarsus and tarsus multi-jointed, long and thin. Pedipalpal coxae movable, separated by a narrow prosternum. Sternal plate separating the pedal coxae of appreciable size. Abdomen flat, elliptic. (Carboniferous and Recent.) Order *Phrynichida*.
 — Pedipalpi not known, except for their coxae, which are immobile, being fused into a single, triangular plate without a trace of a median line. Sternum minute. Lip wanting. Abdomen elongated, more or less cone-shaped, pointed posteriorly. All legs thin and long. (Carboniferous.) Order *Kustarachnae*.
28. Abdominal sternites, except the first and the last, divided by a pair of longitudinal lines into three fields. The first sternite triangular, flanked on its sides by the fourth pedal coxae. The last sternite with a more or less circular anal operculum. Pedipalpal coxae more or less concealed by the first pedal coxae which are movable and may be either contiguous along their mesial edge or slightly diverg-

- ing in front. Rarely the first pedal coxae are quite separated by the pedipalpal coxae. (Carboniferous.) Order *Architarbi*.
- Abdominal sternites entire, without marginal fields 29
29. A well defined sternum present. Chelicerae two-jointed, retrovert 30
- Sternum either not visible or wanting. Chelicerae two- or three-jointed, chelate 31
30. Last sternite with a clearly defined anal operculum. Abdomen always segmented. Soft lateral pleurae present. (Devonian and Carboniferous.) Order *Trigonotarbi*.
- Anus always without an operculum. Abdomen either segmented or without visible segmentation. Lateral soft pleurae wanting. The spinnerets, although they are the most important character of spiders and would make identification certain and simple, seem to be very rarely preserved in Palaeozoic species. (Devonian, Carboniferous, Permian, Tertiary and Recent.) Order *Araneae*.
31. Chelicerae very large, two-jointed, chelate. Arrangement of coxae in Recent species is shown in Figure 24. The ventral surface of the only existing Palaeozoic specimen is not sufficiently well preserved to show the arrangement of the coxae. Abdomen clearly segmented, with soft lateral pleurae. Coxa and trochanter of fourth pair of legs with rackets (malleoli). Mouth at the end of a tubular beak situated between the pedipalpal coxae. (Carboniferous and Recent.) Order *Solifugae*.
- Chelicerae three-jointed, chelate, or situated with the pedipalpi on a distinct capitulum and presenting many modifications of structure. In the second alternative the abdomen shows no segmentation and is completely fused with the cephalothorax 32
32. Chelicerae three-jointed, chelate. Pedipalpi six-jointed and either slender and pediform, or powerful and raptorial. Legs usually long and thin, with coxae approximated or contiguous, the fourth coxae being distinctly the largest. The segmentation of the abdomen is always visible at least in its posterior half. In Recent species the pedipalpal coxae and those of the first and occasionally of the second

pair of legs are with gnathites. (Carboniferous, Jurassic and Recent.) Order *Opiliones*.

- Chelicerae and pedipalpi usually on a capitulum. Chelicerae two-jointed and often greatly modified, pedipalpi often with a reduced number of segments. Coxae often far apart and movable, or approximated, incorporated in the body wall and immobile, but never with gnathites. Abdomen without a trace of segmentation in the adult. (Devonian, Cretaceous, Tertiary and Recent.) Order *Acari*.

CLASS ARACHNIDA

As explained in the introduction, the Class Arachnida is limited here to those Chelicerata which have either book-lungs or tracheal tubes for organs of respiration. The exclusion from the class of Eurypterida, Xiphosura, Pycnogonida and of the still more distantly, if at all related Tardigrada and Linguatulida (Pentastomida), makes the class more uniform and compact. Thus delimited, the Class Arachnida shares with other Arthropoda the possession of a dorsal, ostiate heart and of segmented appendages. It shares with the Crustacea the subdivision of the body into only two portions. With the rest of the Chelicerata the Class Arachnida shares the presence of a single pair of appendages in front of the mouth and the fusion of the deutocerebrum with the protocerebrum. With the nearest related classes, the Eurypterida and the Xiphosura, it shares the possession of only six pairs of cephalothoracic appendages.

The Arachnida differ from the Eurypterida and Xiphosura, besides the possession of book-lungs and tracheal tubes instead of book-gills, in the absence of compound eyes, in the structure of the carapace and in a number of other external and internal characters by which they differ either from the one, or from the other of these two classes.

The earliest fossil records of Arachnida are from the Silurian. Only four specimens as yet have been found. They are primitive scorpions, and are represented by three European and one North American species. In the Devonian of Scotland representatives of three other orders have been discovered, Acari, Araneae and Trigonotarbi. Nine additional orders left fossil representatives in the Carboniferous of Europe and the Pennsylvanian of North America. A representative of the Order Palpigradi, *Sternarthron zitteli* Haase, was discovered

in the Jurassic of Europe; several representatives of the Order Pseudoscorpiones occur in the Oligocene Baltic Amber; and a representative of the Order Schizomida was described from the Coenozoic onyx-marble of Arizona. Although these orders are at present not yet known from the Palaeozoic, there can be scarcely any doubt as to the existence of all sixteen orders at least in the late Palaeozoic. The Mesozoic era left us only three records of fossil Arachnida, the just mentioned representative of the Order Palpigradi, an opilionid, *Hasseltides primigenius* Weyenbergh, and a scorpion *Mesophonus*. Five orders, the Architarbi, Haptopoda, Anthracomarti, Trigonotarbi and Kustarachnae died out in the Palaeozoic.

The class may be divided into four subclasses, of which two died out and two, containing each an extinct order and several orders which survived, increased in the number of their species and form the Recent arachnid fauna of the world. Originally I proposed a subdivision into only two subclasses, the Latigastra in which the juncture between the cephalothorax and the abdomen is of the broad type, and the Caulogastra characterized by the possession of a pedicel. Between these two subclasses, which are still retained here, it became necessary to introduce the new Subclass Soluta in which, as the name implies, the characters are still in a labile state. Some genera have a broadly joined abdomen, others while not petiolated, nevertheless have a connection not wider than one third of their carapace. The number of their abdominal segments also exhibits the same labile condition. This subclass is proposed here for the inclusion of the single Order Trigonotarbi, the representatives of which were previously considered to belong to the Order Anthracomarti. With the final demonstration of the fact that the Anthracomarti, as delimited here, have in addition to a broad juncture of the abdomen, a fixed number of abdominal segments, an arrangement of coxae similar to that in Eurypterida and Xiphosura, and three-jointed chelicerae, it became necessary to break up the old order into two separate orders. With the discovery of the fact that the Haptopoda have a similar arrangement of the coxae and a fixed number of abdominal somites, and that the position of the mouth in these two orders is also different from that in all other Arachnida, it became imperative to segregate them in a new Subclass Stethostomata.

The four subclasses into which the Class Arachnida is divided here, may be separated on the basis of the following characters:

1. Juncture between the cephalothorax and the abdomen of the broad type, with a tendency toward complete disappearance of the first embryonic abdominal somite. Carapace always entire. Chelicerae always in a plane situated dorsad to the other appendages. Ventral surface with either five or four pairs of coxae. I. Subclass *Latigastra*.
2. Juncture between the cephalothorax and the abdomen of the broad type, but without a tendency toward the disappearance of the first embryonic abdominal somite greater than a shortening of its length to some degree. Carapace always entire. Chelicerai coxae in the same plane with the other five pairs of coxae. Mouth situated between the first pedal coxae. II. Subclass *Stethostomata*.
3. Juncture between the cephalothorax and the abdomen variable, either of the broad type or somewhat resembling that of the petiolated type, but then with the first abdominal segment retaining the width of the carapace and the juncture restricted to their median third. Carapace always entire. Chelicerae situated dorsad to the other appendages. Ventral surface with five pairs of coxae separated by a sternum. Mouth ventral, between the pedipalpal coxae. Abdominal tergites divided into three rows of plates. III. Subclass *Soluta*.
4. Juncture between the cephalothorax and the abdomen of the petiolated type, the first embryonic abdominal somite reduced by peripheral constriction to a more or less slender pedicel forming the juncture and wanting only in the Ricinulei, in which the second somite takes its place while the first has completely disappeared. Carapace usually entire, except in three orders in which it is still segmented in its posterior portion. Chelicerae always situated dorsad to the other appendages. The ventral surface always with five pairs of coxae, but the pedipalpal coxae fused in three orders. The position of the mouth is, therefore, variable, characteristic of different branches into which the subclass is divided. A tendency toward the loss of posterior abdominal segments through peripheral constriction is manifested in five orders by the formation of a pygidium and in one order by a corresponding formation of a segmented anal tubercle. IV. Subclass *Caulogastra*.

I. SUBCLASS LATIGASTRA

A few additional remarks concerning the characters of this subclass, given above, may be in place. The status of the abdominal tergites and sternites is different in different orders, but exhibits in all orders the same trend towards the disappearance of the first sternite, a trend which culminates in a complete loss of the first embryonic abdominal somite in scorpions and harvestmen. A strong trend toward a fusion of abdominal tergites with the carapace and of sternites with the ventral wall of the cephalothorax is noticeable in Opiliones and reaches its climax in a complete fusion of the abdomen with the cephalothorax in Acari. Loss of posterior segments is common, but is accomplished by a shortening of segments, and not by a formation of a pygidium brought about by peripheral constriction. The mouth is either in front of or between the pedipalpal coxae. The latter show a tendency toward a displacement dorsad of the first pedal coxae in Opiliones and Architarbi. Of the five orders into which the subclass is divided, the Order Architarbi is the only one which became extinct in the Palaeozoic.

The broad juncture between the cephalothorax and abdomen is undoubtedly a character of the first magnitude. On the basis of that character the Haptopoda and the Anthracomarti could be and actually have been included by me in the Subclass Latigastrea before I realized the importance of the other character which these two orders possess, namely the unusual position of their cheliceral coxae. It could be argued, of course, that that character was of a later origin and that the two orders possessing them could be retained in the Subclass Latigastrea as a branch of it. This may be so, but the cleft between the new Subclass Stethostomata, which I propose for the inclusion of Haptopoda and Anthracomarti, is much deeper than that between even the most distantly related orders of Latigastrea. On the basis of two trends the Latigastrea themselves could be divided into two branches. These trends are: the modification of the mouthparts, accompanied by a dorsad displacement of the pedipalpal coxae, and the fusion of several abdominal segments with the cephalothorax. These trends are manifested by the Opiliones, Architarbi and Acari. In scorpions and pseudoscorpions the mouthparts do not exhibit a trend toward either modification or displacement, and the trend to a fusion of abdominal segments with the cephalothorax was arrested in its course with the loss of the first segment in scorpions and the reduction of the size of the

first sternite in pseudoscorpions. However, it does not seem to me necessary to give names to these branches without much more extensive knowledge of the comparative internal anatomy and development of the living representatives of these orders.

1. Order SCORPIONES

In view of the fact that all scorpions are more or less similar in appearance, their confusion with other Arachnida is impossible. Even their distinction from scorpion-like Eurypterida is not difficult. The usual definition of the order is therefore limited to externally visible characters and an account of distinctive features of their internal organs may be found only in larger treatises, in the chapters dealing with such organs. Yet an understanding of the origin and relationships of an animal group is not possible without reference to comparative anatomy and embryology. To fill out this gap in definitions usually found in taxonomic monographs and average textbooks of zoology, a brief account is given here of such distinctive internal characters and of external characters which are either not plainly visible or else cannot be correctly interpreted without knowledge of their embryonic development.

Mouth antero-ventral in position, situated between the bases of the pedipalpal coxae, bordered in front by the anterior lip (called also upper lip, labrum, camarostome or rostrum) and behind by the posterior lip. Pharynx spacious and well developed, gizzard weak and not very different from the oesophagus. Midgut with two pairs of branched thoracic diverticles similar to the abdominal five pairs. Anus without an operculum. Maxillary glands only in the maxillary lobes (gnathites) of the first and second pair of legs, none in the pedipalpal coxae.

Thoracic coxal glands each with a single outlet at the base of the third pedal coxae.

Heart restricted to abdomen, with seven pairs of ostia in the preabdomen.

Genital opening in both sexes immediately behind the sternum, provided with a pair of opercula, belonging with its corresponding sternite to the second embryonic somite. Male with a pair of copulatory organs protrusible through the genital opening. Testes in the shape of a single, fenestrated organ consisting of three longitudinal and five transverse, anastomosing ducts. Ovary of the same, fenestrated type.

Respiration by means of four pairs of book-lungs belonging to the fourth to seventh embryonic somites.

All twelve abdominal neuromeres persisting in the adult, but the first four withdrawn into the thorax, the twelfth into the penultimate abdominal segment and fused with the eleventh; the intermediate neuromeres also more or less displaced.

The tergite of the first embryonic somite persists in the extinct *Protoscorpiones*, but is wanting in all *Euscorpiones*. In the latter the first visible tergite is therefore in reality the tergite of the second embryonic somite. The normal number of abdominal segments is restored by subsegmentation of the 8th (last preabdominal) somite and is an older character than the loss of the first somite, since it is present already in the *Protoscorpiones*.

Key to Families of Fossil Scorpions

1. Preabdomen still composed of eight segments. The first tergite either concealed under, but still visible through the carapace, or fully exposed. Suborder *PROTOSCORPIONES*, new 2
 - First preabdominal segment completely lost. Only seven tergites present. Tarsi with two claws. Suborder *EUSCORPIONES*, new 3
2. Legs with very short joints, the femur no longer than the trochanter and about as long as wide. Tarsi ending in a sharp point. Sternum pentagonal. Fourth coxae abutting against the anterior, converging sides of the sternum; third coxae meet in median plane in front of the sternum. First abdominal tergite concealed under the carapace, outlined by a transverse furrow of the latter. Silurian, European and North American Family *Palaeophonidae*.
 - First tergite fully exposed. Appendages with more elongated joints. North American, Pennsylvanian. Family *Mazoniidae*.
3. Third and fourth coxae abutting against the sternum 4
 - Third coxae abutting against the sternum, fourth coxae against the genital operculum Family *Isobuthidae*.
4. Legs short, fourth pair not reaching the middle of the last preabdominal segment. Hand fairly short and stout, with comparatively short fingers. Family *Archaeoctonidae*, new.
 - Legs fairly long, fourth pair reaching beyond the end of the preabdomen. Hand with more or less long fingers 5

5. Anterior end of carapace bluntly pointed. Width of hand three and a half times smaller than its length from the articulation with the patella to the end of the finger

Family *Cyclophthalmidae*.

- Anterior end of carapace either evenly rounded or transversely truncated, often even slightly emarginate. Hand from four to eight times longer than wide

Family *Eoscorpionidae*.

1 Suborder PROTOSCORPIONES, new

1 Family PALAEOPHONIDAE Thorell and Lindström

With the characters given in the key.

Genus *Palaeophonus* Th. & L., 1884.

Syn. *Proscorpius* Whitfield, 1885

Type *P. nuncius* Th. & L.

To this genus belong three Silurian species, *P. nuncius*, *P. caldonicus* and *P. osborni*.

Palaeophonus nuncius Th. & L.

Palaeophonus nuncius is known from a single specimen found in Gotland 120 feet above the sea "in a stratum of thin marly clay, of Ludlow age." Thorell and Lindström gave a detailed and excellent description and figures of the scorpion in 1885. Only the anterior piece of the scorpion is reproduced here photographically from the original plate (Figure 170). The authors (134) gave careful measurements of all parts in millimeters. The total length of the specimen is given as 62 mm. Of special interest are the following statements.

"We have not been able to detect, in our scorpion, any traces either of *dorsal* or of *lateral eyes*, and it is therefore doubtful whether it was provided with visual organs, which are present in the *Palaeophonus* found in Scotland by Dr. Hunter," (p. 10).

"Parallel with its posterior margin, the cephalothorax shows a broad and strong transverse furrow, which extends nearly to the lateral margins, where it either expands to form a triangular figure, or is slightly bifurcate; the furrow is very shallow in the middle and is produced a little forwards, so as to form a very obtuse angle. The part of the cephalothorax behind this furrow is, in the middle, about one fourth of the total length of the cephalothorax: *it much resembles a separate segment, having nearly the same length in the*

middle as the first dorsal plate of the abdomen." (p. 9. Italics are mine, A.P.)

"The *walking limbs or legs* (fig. 1, $P_1 - P_4$) are altogether different in form from those of modern scorpions, though composed, as in these latter, of seven joints . . . The legs are short and dumpy tapering at first (to the base of the fourth joint) slightly, then rather strongly toward the tip, *which is pointed, and destitute of the two movable claws with which other scorpions are provided* . . . The joints, in the different pairs of legs, are very nearly of the same form. They were probably, with the exception of the coxa and the last tarsal joint, cylindrical or nearly so, whereas, in recent scorpions, the thighs and the tibiae are compressed and, moreover, much longer than in *Palaeophonus* . . . The hindmost coxae are probably much shorter in *Palaeophonus* than in recent scorpions." (p. 11).

"By far the most important of these deviations occurs in *the form of the legs*, a form so peculiar and so decidedly unlike what has hitherto been met with in this group of animals, that one might have felt uncertain whether *Palaeophonus* really is an arachnid, had not its perfect conformity with the scorpions in all other essential points, and especially in the presence of stigmata (*spiracula*) on the ventral plates, excluded every doubt concerning its systematic position." (p. 18). "Another very important feature, by which *Palaeophonus* (at least the Scotch species, according to Peach) differs from both recent and Carboniferous scorpions, may be observed in the arrangement of the posterior coxae: for whilst in *Palaeophonus*, only the coxae of the fourth pair abut against the sternal plate, which is bound along its anterior margin by the coxae of the third pair; in other scorpions the coxae of *both* these pairs abut against the sternum, which is bounded in front by the coxae of the second pair." (p. 18). (Compare this statement with the characters of the Family *Isobuthidae*, A.P.)

Palaeophonus caledonicus Hunter, 1886

(syn. *P. hunteri* Pocock, 1902).

The Scottish Silurian scorpion is also represented by a single specimen found by Hunter in 1883 at Lesmahago, Lanarkshire: it was described and figured by Pocock; was lost, according to Bather "in the ashes of Kilmarnock Museum" but seems to have been again recovered. Pocock's figure is reproduced here photographically (Figure 172). Pocock gives the length of the specimen as 35.5 mm.

Of interest to us here are his following statements. "In the Scotch specimen also there is no sign of the lateral eyes. If, however, as is possible, these organs existed, and were placed behind the level of the median eyes, as is the case in the normal Pedipalpi, and, as is alleged, in the Carboniferous *Anthracoscorpium*, they would be concealed from view beneath the basal segments of the anterior legs, which on each side overlies that portion of the carapace immediately behind the median eyes. The median eyes are very distinctly represented by a pair of elliptical impressions situated close together, one on each side of the middle line, and scarcely more than their own long diameter from the anterior border of the carapace. There is no evidence that these eyes were elevated upon a tubercle." (p. 293).

"Nor was I able to detect a sign of the presence on the fifth segment of any of the legs of that spur so clearly shown on the first, second, and third pairs in the Gotland fossil, and described and figured by Thorell." (p. 297).

"I found no distinct traces of stigmata in the Scottish specimen." (p. 306).

Palaeophonos osborni Whitfield, 1885.

Syn. *Proscorpius osborni* (Whitfield).

This species is represented by a single specimen discovered in 1882 by Mr. A. O. Osborn in the waterlime of Waterville, Oneida Co., N. Y. The first announcement of the find was made by Whitfield in *Science* in 1885 and the specimen referred to *Palaeophonos*. In the same year the new Genus *Proscorpius* was proposed by Whitfield, because of the supposed presence of double claws on the walking legs. This character was later shown by Thorell and others to be spurious. The leg is incomplete and what look like claws are in reality pointed ends of a broken joint. Nevertheless, Clarke and Ruedemann (10) left the genus without synonymising it with *Palaeophonos*. They gave a detailed description of the specimen and excellent figures. Unfortunately some of their statements are based on misinterpretation of visible structures. Owing to the courtesy of Dr. Otto Haas, Curator of Invertebrate Paleontology in the American Museum of Natural History, to whom my sincere thanks are due, I was able to study the specimen in my own office in New Haven. A photograph which I made of the specimen is shown in Figure 189. The following description of the type is the result of my own study.

Carapace ca. 4.0 mm. long, ca. 4.0 mm. wide at posterior edge. Exact measurements are impossible because the right posterior corner

of the carapace is not fully visible, while the outline of the anterior edge is not quite clear. The latter seems to be convex. The eye-tubercle is flat, sub-pentagonal, with a procurved posterior edge and rounded corners. No eyes or anything resembling eyes can be seen either on the eye-tubercle or on the posterior portion of the carapace as figured by Clarke and Ruedemann, no matter how the light is arranged, what the angle of the incident rays may be, whether the light is monochromatic green or allowed to pass through a deep yellow filter, or used without any filter, whether the specimen is examined dry or wetted with alcohol. *There are no eyes.*

The surface of the carapace has the same texture as the two exposed abdominal tergites, i.e. it appears to be finely mottled with white. About 0.86 mm. in front of the posterior edge of the carapace a transverse sulcus across the entire width of the carapace is visible. The sulcus is shallow, but well defined, parallel to the straight posterior edge of the carapace. Assuming, as I believe to be correct, that it marks the anterior edge of the first tergite concealed under the carapace, we find that the preabdominal tergites increase in length as one proceeds backward. The following measurements of their length show this clearly in millimeters. (1) 0.86; (2) 1.29; (3) 1.71; (4) 2.29; (5) 2.57; (6) 2.71; (7) 2.86; (8) 3.86. The segments of the postabdomen measure respectively 2.86-2.86-3.29-3.29-? (only a small portion of the fifth segment is preserved). The width of the preabdominal tergites is (1) ca. 4.0, (2) 4.29, (3) 7.29, (4) 8.57, (5) 8.43, (6) 8.14, (7) 7.24, (8) 6.14. Width of postabdominal segments 2.86-2.43-2.29-2.00-? Hand 5.43 long, 2.00 wide. Fingers 4.00 long, slender, both curved in the same sense. Neither teeth, nor any granules on fingers visible. The arm is short, but cannot be measured because at least two other appendages are superimpressed over it.

The second and third postabdominal segments are with a pair of longitudinal grooves, the fourth segment with a pair of longitudinal ridges. The first segment alone has a single, more or less median longitudinal groove.

The single preserved chelicera is wide and short. No claws can be seen on any of the three limbs, which are not complete.

On the right side of the specimen six plates are visible, projecting from under the broken edge of the tergites. Their edge is exactly in the line in which the edge of the corresponding tergites would be and their length is the same as that of the overlying

tergites. Their nature was the subject of controversy in the past. The objections of Thorell, Pocock et al. to Whitfield's interpretation supported by Scudder, that these plates are true sternites, seem to me to be well founded. It is certain that in no Recent scorpions do the anterior two sternites project as far laterally. The sternite corresponding to the first visible tergite is reduced in them to the genital opercula, the third to the median plate to which the combs are attached. In *Palaeophonus caledonicus* (Figure 172), the only species in which these sternites are preserved, they have the usual appearance. On the other hand I cannot accept as correct the interpretation that the projecting plates are pieces of the tergites themselves, broken off and pressed in. If that were so, they would have the same texture as the rest of the tergites. As a matter of fact their color is somewhat different from that of the overlying plates. In some places one can see that they continue *under* the latter. This was confirmed by removing a minute piece of one of the tergites. The thickness of the layer contained between the two surfaces is a fraction less than 0.2 mm. This is not very different from the average thickness of a tergal plate of Recent scorpions. I think we may conclude from these facts that the main portion of the tergites represents a mold of their *dorsal* or outer surface, while the projecting lateral portions represent the *ventral* or inner surface of the same tergites.

The three species of *Palaeophonus* may be distinguished as follows, by assuming the correctness of published descriptions:

1. No ocular tubercle, but a pair of elliptical eyes present, situated scarcely more than their own long diameter from the anterior border of the carapace. *Palaeophonus caledonicus* Hunter.
- A distinct eye-tubercle present at anterior end of carapace, but eyes are wanting 2
2. Carapace a little over 8 mm. long. The movable finger a little over 8 mm. long. *Palaeophonus nuncius* Th. & L.
- Carapace ca. 4 mm. long. Movable finger 4 mm. long. *Palaeophonus osborni* Whitfield.

Genus *Dolichophonus*, new

Type *D. loudonensis* (Laurie, 1898, sub *Palaeophonus*)

This genus differs from *Palaeophonus* by the shape of its carapace, for whereas in the latter the carapace is as long as wide, in *Doli-*

chophonus it is appreciably longer than wide and the proportion of the two preserved segments of legs are also much longer than wide.

Dolichophonus loudonensis

Trans. R. Soc. Edinburgh, Vol. 39, pp. 576-578, Pl. I, fig. 1.

The only specimen of this species is in the Edinburgh Museum of Science and Art. Laurie's figure is reproduced here photographically (Figure 171). According to Laurie the "carapace is 10 mm. long and 7 mm. wide. The anterior margin is distinctly concave, and the sides almost parallel, but slightly convex. The posterior margin appears fairly straight. Situated about 1 mm. from the anterior border is a double depression, which I take to mark the position of the median eyes. If they correspond in size to these depressions they must have been very large . . . There is a slight roughness at the left anterior corner of the carapace, which probably marks the position of the lateral eyes." (p. 577).

"The last five segments are even more obscure than the rest of the specimen. The tail, which they constitute, appears to have been narrow (2.5 mm.) and long, though it is difficult to estimate the length of the whole . . . The tail segments appear to have been ornamented with longitudinal ridges possibly composed of a series of knobs." (p. 578).

The specimen was found by Mr. Hardie in the Pentland Hills of Scotland.

2 Family MAZONIIDAE Petrunkevitch

The characters of this family are given in the key. A single Genus *Mazonia* with a single species *Mazonia woodiana* M. and W. represented by a single specimen, belongs to this family. It was found in the Pennsylvanian of Mazon Creek, Illinois, and is in the collection of the University of Illinois. A full quotation of its original description by Meek and Worthen was given in my Monograph (93) on page 54 and a photograph of the specimen is reproduced here in Figure 13 on Plate III.

The interpretation given by me at that time appears to me now to be wrong. Then the fact of the subsegmentation of the eighth embryonic abdominal somite was not yet discovered and the true story of segmentation in scorpions not known. My assumption of that time, that *Mazonia* either had a tail of only four segments or no distinct separation between the preabdomen and the postabdomen

cannot be accepted now in the light of our present knowledge and of what I have explained above in the present paper. *Mazonia* must have had a tail composed of the usual five segments, but the first preabdominal tergite was still in existence and was fully exposed in *Mazonia*, a character by which the Family *Mazoniidae* differs from the Family *Palaeophonidae* in which that tergite is concealed under the carapace.

Mazonia hungerfordi Elias, from the Pennsylvanian of Kansas, is not a *Mazonia*, as far as one can judge from the rather brief description, and cannot be placed. The specimen is in the collection of the University of Kansas.

The True Nature of the Primitive Scorpions

Thorell and Lindström laid great stress on the presence of spiracles in *Palaeophonus nuncius*. Although they recognized the arachnid nature of the creature, they pointed out the presence of some features by which it differed from other scorpions. They felt certain that they had before them an air-breathing, primitive scorpion. On the other hand Pocock (105) expressed "the belief that *Palaeophonus* lived in the sea, probably in shallow water, its strong, sharply pointed legs being admirably fitted, like those of a crab, for maintaining a secure hold amongst the seaweed or on the jagged surface of rocks, and for resisting the force of the rising and falling waves." (p. 306). He suggested that what Thorell regarded as spiracles were not such and that the one which was figured by Thorell is only a "fortuitous crack." He further tried to use the apparent lack of spiracles in the two specimens of *Palaeophonus* as evidence that both species did not have stigmata and did not breathe air by means of book-lungs, but that their respiration "may have been effected by means of the appendages of the second mesosomatic somite, although it must be admitted they appear too small to have performed this office for the whole organism without help from other organs. It is possible that there were such organs in the form of small appendages bearing branchial lamellae attached to the mesosomatic sterna. But if so, no definite trace of such has been preserved." (p. 307).

Clarke and Ruedemann (10) reexamined Pocock's arguments and came to the following conclusion. "It would be singular indeed if, of all the Siluric terrestrial fauna, the scorpions alone should have been repeatedly carried out to sea in a good state of preservation; much more plausible is the assumption of their coexistence

in the sea with the similarly constructed and closely related eurypterids, with which their remains are found associated." (p. 400).

Since the publication of Clarke and Ruedemann's celebrated work (10) from which the above quotation is taken, the attitude of specialists toward the habitat of Eurypterida underwent a considerable change. Writing in 1944, the distinguished Scandinavian paleontologist Størmer (129) says: "The eurypterids are chiefly known from fresh-water and brackish-water sediments of the late Silurian and Devonian" . . . "The absence of eurypterids in typical marine faunas, and their presence in continental sediments show that they lived in fresh or brackish water . . . The Stylonuridae . . . were evidently typical benthonic forms. They probably walked like terrestrial arachnids with the abdomen in an elevated position. Possibly some species occasionally might endure the life on land (the gills are well concealed below the abdominal appendages). Many of the other eurypterid genera were also bottom dwellers." (p. 49).

It is true that the pointed tarsi of *Palaeophonus* resemble those of crabs. But we know Recent crabs which live on land and even climb trees. At the same time we know typical arachnids which live in water yet are dependent on respiration in the air and possess either book-lungs, or tracheal tubes, or both, but no gills adapted to aquatic respiration. Patient and careful search for organs of respiration in fossil Arachnida of all orders, including all known North American specimens and the rather rich European collection of the British Museum convinced me that it is a rare case, indeed, when a spiracle is preserved well enough to be recognized as such beyond any possibility of doubt. I have not seen a single spiracle in any North American Paleozoic scorpion, nor in any European one which I have studied. Neither did Pocock describe any in the specimens which he studied. Peach (91) in describing new species of fossil scorpions says on page 399 concerning *Eoscorpheus tuberculatus* "Within the rounded postero-lateral angles of this plate (third ventral plate, A.P.) two fine slits occur which are the openings into the air sacs." In describing *Eoscorpheus glaber* on page 400 Peach says: "Slit-like spiracles, surrounded with a raised margin, have been observed within the postero-lateral angles of those of the third and fourth segment," and he states further: "I have endeavoured to represent the appearance of the fossils to the naked eye as truthfully as possible in figs 2 and 2a." These figures do not show the spiracles, but a spiracle is shown enlarged 3 diameters in figure 2m.

Fritsch figures several spiracles, but their shape is so different from anything known in Recent or fossil scorpions that it is not advisable to use them as evidence without reexamination of the specimens.

These seem to be all the data available concerning the spiracles of Palaeozoic Arachnida. It is clear that the absence of spiracles in fossil scorpions cannot be used as evidence of aquatic respiration. This question can be answered only on the basis of comparative morphology. In every detail of its structure *Palaeophonus* resembles other scorpions much more than it does Eurypterida or Crustacea. It differs from other scorpions only by the pointed shape of its tarsi and lack of tarsal claws. All Arachnida are adapted to aerial respiration. Some Acari may receive their oxygen by diffusion through the skin or through the wall of the alimentary tract, but even these minute and highly aberrant forms lack gills. The coexistence of Silurian fossil scorpion remains with eurypterids may be attributed to their life in the proximity of fresh or brackish water or even to more or less prolonged sojourn between tides as in the case of several species of Recent spiders, without the necessity of postulating aquatic respiration. All available evidence considered, the primitive scorpions must be regarded as air-breathing Arachnida unless new, incontrovertible evidence is produced.

2 Suborder EUSCORPIONES, new

This suborder includes all Recent and fossil scorpions in which the first abdominal embryonic somite has completely disappeared and is represented in the adult only by its neuromere incorporated in the ventral, thoracic ganglionic mass. The classification of Recent scorpions is still in a very unsatisfactory state. It is based entirely on external characters, such as the shape of the sternum, of the number of tarsal thorns or spurs, the structure of the comb, the rows of granules on the fingers, etc. It is possible that some day this classification will prove to be natural, but this is very doubtful. At least in the case of the sternum I have shown (95) that it changes its shape from that of a pentagon in the embryo to a triangle in the adult. Of the comparative internal anatomy of scorpions we have absolutely no information. If in Palaeozoic fossils all external characters were preserved, no matter how unsatisfactory the classification of Recent scorpions may be, it should be used whenever possible. Unfortunately even this cannot be done. In 1913 I proposed a classification which seemed to meet the require-

ments at the time. It is not satisfactory at present and should be discarded in favor of the one proposed here, until a better one can be found.

The arrangement of the coxae is peculiar only in the Family *Isobuthidae* and resembles that in *Palaeophonidae*. The fact that the fourth coxae abut against the genital operculum and not against the sternum, as in all other fossil and Recent scorpions, is not to be mistaken for a primitive character. On the contrary, remembering that the genital operculum represents the second abdominal embryonic somite, we must admit that the latter moved in *Isobuthidae* and *Palaeophonidae* even further forward than in other scorpions. In fact, it moved as far forward as it possibly could, emphasizing the other fact that some evolutionary trends reached a climax already in the Palaeozoic.

The erection of the new, fossil Family *Archaeoctonidae* on the basis of the shortness of the appendages seems to me reasonable, because of its isolated occurrence. It is impossible to say whether it is an ancestral character which contributed to a relatively early extinction of the family, or a trend newly acquired and unfavorable to survival.

With the removal of three genera from the Family *Cyclophthalmidae* into the new Family *Archaeoctonidae*, it became necessary to base the separation of the *Cyclophthalmidae* from the *Eoscorpionidae* on other characters than those used by me in 1913. They include the shape of the carapace and of the hand.

1 Family ISOBUTHIDAE Petrunkevitch

Although the collection of the British Museum, now before me, does not contain any representatives of this family, I reproduce here my old key to genera, because it applies to both North American and European fossils and may be of use to other investigators.

Key to Genera

1. Abdominal sternites with straight posterior edges. Sternum triangular. Genus *Palaeobuthus* Petrunkevitch. A single species, *P. distinctus* Petrunkevitch, from Mazon Creek, Illinois.
- Abdominal sternites with posterior edges curved, so that the sternites appear bilobed 2
2. Sternum rhomboidal. Genus *Isobuthus* Fritsch.

A single species, *I. kralupensis* (Th. & L.) from the Coal Measures of Kralup, Bohemia.

— Sternum oval. Genus *Eobuthus* Fritsch.

Three species.

1. *E. rakovnicensis* Fritsch. Type from the Coal Measures of Rakonitz, Bohemia. The specimen described by Wills from the Oranje Nassau Mine III belongs probably to this species.
2. *E. holti* Pocock from Sparth, near Rochdale, England. The specimen from Preesgweene near Chirk collected and studied by Wills seems to belong to this species.
3. *E. pottsvillensis* Moore, from the Pottsville formation, in the basal portion of the Carboniferous series, of Clay County, Indiana, U.S.A. A single specimen.

2 Family ARCHAEOCTONIDAE, new

The characters of this family are given in the key. They are the unusual shortness of the limbs and of the hand. Taken in themselves they would be insufficient for the separation of Recent scorpions. But their general appearance is so different from other scorpions found in the Coal Measures, that in the absence of other characters, because of poor preservation, it still seems reasonable to segregate them in a family distinct from those with more or less normal proportions. I refer three genera to this family, *Archaeoctonus*, *Palaeomachus* and *Eoctonus*. They may be distinguished as follows.

1. Fifth postabdominal segment much longer than the fourth.
The fingers of the hand straight. Genus *Eoctonus* Petrunkevitch with a single species, *E. miniatus* Petrunkevitch from Mazon Creek, Illinois (1913).

— All postabdominal segments of about the same length.
Fingers curved 2

2. Movable finger about equal in length to the width of the hand. Genus *Palaeomachus* Pocock.

— Movable finger much longer than the width of the hand.
Genus *Archaeoctonus* Pocock.

Genus *Palaeomachus* Pocock, 1911

Type *P. anglicus* (Woodward), sub *Eoscorpheus*

Pocock gave the characters of this genus on p. 16 and assigned a single species to it. I refer to the Genus *Palaeomachus* specimen

In. 13976 of the British Museum, from the Coal Measures of Coseley, Staffs. The specimen consists of two pieces, both showing only the hand, photographically reproduced in Figure 180. Figure 156 shows the hand magnified six diameters for comparison with *P. anglicus*, the hand of which is shown in Figure 155, copied from Woodward with omission of the other segments of the appendage and brought to the same size as Figure 156. The resemblance is not great and the generic affiliation of our specimen is far from certain, but in the absence of any other characters it must stand for the present, because the hand resembles other species still less than it does *Palaeomachus*. The measurements of the hand are as follows: total length from the proximal end to the end of the movable finger 13.0 mm., width 5.3 mm., movable finger 7.8 mm. long. If the proportions of the body and limbs of this fossil are the same as those of *Archaeoetonus*, as seems to be reasonable to expect, then the total length of the animal must have been about 60 mm.

Genus *Archaeoetonus* Pocock, 1911

Type *A. glaber* (Peach), sub *Eoscorpis*

This genus was proposed by Pocock (111) who gives a definition of it on page 17. He referred to this genus with some reservation, also the species described by Peach under the name of *Eoscorpis tuberculatus*. Both species were found in calciferous sandstone of the Lower Carboniferous. I refer to the latter species, also with reservation, specimen No. 988 in the British Museum collection, represented by a single piece from the Lower Carboniferous of "Eskdale, N. B.," purchased of R. Damon on April 27th, 1885. It is a poorly preserved specimen shown in Figure 138 and photographically in Figure 176. The fifth postabdominal segment and the poison gland are missing, as are all appendages with the exception of a few indistinct pieces on the left side belonging presumably to the pedipalp. Assuming that the missing end of the specimen was as long as the two preceding segments, we may estimate the approximal total length as 21 mm. The carapace is very indistinct, its surface covered with coarse punctures. Peach describes and figures a pair of eyes, but no trace of eyes can be found in our specimen. However, the lack of eyes in this case cannot be attributed to their non-existence, because the preservation of the surface is too imperfect to warrant the validity of a negative observation. The pre-

abdominal tergites are clearly visible and conform more or less with Peach's description. The tail shows that its first and second segments were shorter than the following ones. The color of the specimen is the same as that of the matrix, i.e. a dull and very dark grey, almost black, except in a few spots where the chitin is miraculously preserved.

3 Family CYCLOPHTHALMIDAE Petrunkevitch, 1913, emended

This family was proposed by me for the inclusion of four genera, three of which are here placed in the Family *Archaeoctonidae*. This leaves only two species of the Genus *Cyclophthalmus*, as then defined, in the family, namely *C. senior* Corda and *C. euglyptus* (Peach). Pocock (111) states on p. 12 that "the species, described as *Eoscorpium euglyptus*, has the large chelicerae and stout chelae of *Cyclophthalmus*, and I am unable to say that it does not belong to that genus." Pocock overlooked the fact that Thorell and Lindström proposed in 1884 the Genus *Centromachus* for *Eoscorpium euglyptus* and four other species described by Peach under the Genus *Eoscorpium*. I, too, was not aware of this fact in 1913. Perhaps both Pocock and myself were taking it for granted that Fritsch's reference in 1904 to *Centromachus* as a synonym of the eurypterid Genus *Glyptoscorpium* was correct. Fritsch (23) writes on page 77: "Die Aenderung des Gattungsnamens *Glyptoscorpium* in *Centromachus*, welche Thorell vornahm, war ziemlich unnütz, denn es handelt sich hier nur um Fragmente von Segmenten eines zu den Pterygoten gehörigen Thieres und um keinen Scorpion, weshalb wir uns hier damit nicht zu befassen haben." Fritsch does not state where Thorell published the name *Centromachus* for the first time, nor how he himself came to the conclusion that the fossil for which the genus was proposed, was a remnant of a pterygote. The real facts are as follows: Thorell and Lindström (134), discussing the affinities of *Palaeophonus* with other scorpions, wrote in their celebrated paper "On a silurian Scorpion from Gotland" on page 21: "Very different, and no doubt even generically distinct forms have been united under *Eoscorpium*. We have already mentioned the difference in the shape of the cephalothorax of for instance *E. inflatus* Peach and *E. tuberculatus* Id., as well as the great dissimilarity in the number of the rows of the pectinal lamellae of *E. carbonarius* Meek & Worthen and *E. euglyptus* Peach, which latter species, in consequence of this difference, may be made the type of a new genus (*Centromachus* n.), to which

also the other species of *Eoscorpis* described by Peach, and possibly also *E. Anglicus* Woodw., may provisionally be referred."

In the same paper Thorell and Lindström give in the chapter on the classification of the scorpions the characters by which their new family *Cyclophthalmidae* may be separated from Scudder's Family *Eoscorpoidae* and the character by which *Centromachus*, placed in the latter, may be separated from *Eoscorpis*. According to them, *Eoscorpis* has "no intermediate lamellae in the combs," while in *Centromachus* the "combs (are) provided with numerous intermediate lamellae." This character separates *Centromachus* also from *Cyclophthalmus* to which Thorell and Lindström refer three species, because in that genus there are "no intermediate lamellae (plates between the rhachis and the fulcra of the comb-teeth)." The characters given by Thorell and Lindström for the separation of the two families are not valid today because of the incorrect and altogether fanciful description of the eyes in the type of *Cyclophthalmus* given by Corda in 1835 when he established the genus. But this is beside the point here, for all that we are interested to know is whether the Genus *Centromachus* is valid. The above quotations show this to be so beyond any possibility of doubt, because *Eoscorpis euglyptus* Peach for which the Genus *Centromachus* was proposed, is an almost completely preserved scorpion with all the characters of scorpions and not pieces of segments of a pterygote, as Fritsch states.

The character used by Thorell and Lindström for the separation of their new genus *Centromachus* from *Eoscorpis* is also not valid any more. Poor preservation and lack of material were responsible for this supposed distinction. I have given in the key the only characters by which the two families may be separated and while I still do so, I think that unless new characters will be found, the two families will have to be merged into a single family.

Fritsch (23) studied the type specimen of *Cyclophthalmus*, exposed the preabdomen and a portion of the postabdomen, gave a photographic reproduction of the specimen in his figure 84 on page 67, figures of it on Plate 7 and reconstructions in figures 85 and 86. Concerning the comb he says "Von den Kammorganen sind an derselben Figur nur ganz schwache Reste wahrnehmbar." (p. 68). And since the comb is so poorly preserved, it evidently cannot be used as a character. Pocock (111) states on page 20 (1911) "*C. senior*, the type of the genus *Cyclophthalmus*, certainly differs from *C. euglyptus* in having the hand shorter, the movable digit being much longer than

the back of the hand. So far as size is concerned, the two Scorpions are much alike." Provisionally, then, this character alone can be used for the separation of the two genera.

Genus *Cyclophthalmus* Corda, 1835

Type *C. senior* Corda

For description of this species see Fritsch (23)-66.

Genus *Centromachus* Thorell and Lindström, 1884

Type *C. euglyptus* (Peach), sub *Eoscorpins*

I refer to this genus and species specimen In. 12849 of the British Museum, represented by a single piece from the Lower Carboniferous of Langholm, Dumfriesshire. It is shown in Figure 136 and photographically reproduced in Figure 173. The color of the specimen is the same as that of the matrix, a dull slate grey, almost black, except in a few small places where the chitin is still preserved. Only the coxa is missing, and the tip of the immobile finger is broken off. The shape of all joints is best understood from the drawing which was made with the aid of a camera lucida without any difficulty because of the excellent preservation. The dotted lines merely show the limits of the surfaces without remnants of chitin. There are bead-like tubercles on the hand and somewhat less regular ones on the femur. The patella is about of the same length as the femur and about as long as the hand to the base of its finger. The total length of the hand from its proximal end to the tip of the movable finger is 9.0 mm., of the movable finger 5.0 mm. The width of the hand is 2.86 mm., of the patella 2.29 mm. The shape of the hand and its fingers conforms fairly well with the figure given by Peach for his type.

4. Family EOSCORPIONIDAE (=Eoscorpionidae) Scudder

The characters of this family are given in the key and their value discussed in the remarks concerning the Family *Cyclophthalmidae*. The limits of the family remain the same as in my Monograph of 1913. But the Genus *Microlabis* Corda is omitted and seven new genera added. The position of *Microlabis* is quite uncertain. Without a study of the original specimen the genus cannot be placed in the system proposed here for the separation of genera. Fritsch redescribed the original specimen, gave figures of it on Plate 9 and a restoration of the dorsal surface in Figure 87 on page 69, but neither his descrip-

tion, nor his figures can be incorporated in a key. The latter is now based almost exclusively on the structure of the carapace, this being the safest and most easily available character in fossil scorpions.

Key to Genera of the Family Eoscorpionidae

1. Blind scorpions, definitely without eyes 2
- Scorpions with eyes 4
2. Carapace distinctly wider than long, with converging sides; front rounded. Preabdominal tergites all of about the same length (Figure 137). Genus *Anthracoscorpio* Kusta.
- Carapace not wider than long 3
3. Carapace as wide as long, more or less truncated in front, with cephalic portion high, extending almost to posterior border and subdivided by a forked groove into three portions: an anterior central and a pair of lateral ones (Figure 146). Genus *Typhloscorpium*, new.
- Carapace unusually large, being about two-thirds as long as the preabdomen, and flat. Postabdomen reduced to the size of even a shorter and thinner tail than in the Recent *Opisthacanthus* (Figure 143). Genus *Typhlopisthacanthus*, new.
4. Carapace triangular, with a pair of elliptical eyes on a tubercle situated close to anterior edge. Genus *Trigonoscorpio* Petrunkevitch.
- Carapace not as above 5
5. Carapace high, considerably wider than long, and wider behind than in front (Figure 139). A pair of elliptic eyes on a transverse tubercle situated close to anterior edge. Cephalic portion of carapace extends almost to posterior edge. Genus *Lichnophthalmus*, new.
- Median eyes circular when viewed in the line of their axis 6
6. Carapace as wide as long or distinctly longer than wide 7
- Carapace distinctly wider than long 8
7. Median eyes close to anterior edge which is evenly rounded (Figure 140). Fingers of the hand reach to end of third postabdominal segment. Genus *Europhthalmus*, new.
- Median eyes at a considerable distance behind the anterior

- edge which is truncated and slightly concave. Fingers of hand not reaching beyond middle of second postabdominal segment. Genus *Eoscorpius* Meek and Worthen, emended.
8. Postabdomen slender and short. Carapace trapezoidal, with rounded corners. Genus *Palaeopisthacanthus* Petrunkevitch, emended.
- Postabdomen normally developed 9
9. Carapace fairly rectangular, with slightly converging sides and an almost straight anterior edge. Genus *Alloscorpius*, new.
- Carapace evenly rounded in front 10
10. Carapace nearly semicircular, flat, without margins. Eye-tubercle and lateral eyes wanting. Median eyes sessile (Figures 144-145). Genus *Lachnoscorpius*, new.
- Carapace with converging sides, rounded in front (Figures 147-150) distinctly margined, its surface slightly elevated in middle and visibly sculptured. Eye-tubercle longitudinal. Lateral eyes present, situated slightly in advance of the median ones. Genus *Compsoscorpius*, new.

The Genera *Feistmantellia* Fritsch and *Microlabis* Corda have not enough distinctive characters for inclusion in the key.

Genus *Anthracoscorpio* Kusta, 1888

Type *A. juvenis* Kusta

This genus was proposed by Kusta for a specimen originally mentioned by him as a young *Cyclophthalmus senior*. Fritsch (23) gave a drawing of the type in his Figure 94 on page 76. There seems to be no evidence whatsoever to assume that the fossil was a young scorpion. In recent young scorpions the proportions of the body differ from those of the adult in the first instar and somewhat in the second instar. The specimen shown in Fritsch's Figure 94 has a fully distended preabdomen and resembles a mature female more than a young individual. Pocock uses the genus for inclusion of species which certainly do not belong to it if one considers the characters of the type specimen. Since the collection of the British Museum contains a fossil scorpion remarkably similar to Kusta's *Anthracoscorpio juvenis* and has certainly no eyes, I thought it advisable to limit Kusta's genus to the single species for which it was proposed.

Anthracoscorpio juvenis Kusta, Sitz. ber. d. k. böhm. Ges.
der Wissensch., 1888, p. 206.

Fritsch, Pal. Arachn., 1904, p. 75, Figure 94

I refer to this species specimen No. 39764 of the British Museum from the Lower Carboniferous, calciferous sandstone series of Eskdale, N. B. It is represented by a single piece shown in our Figure 137 and photographically in Figure 175. The fossil is of the same color as the matrix, i.e. a dark slate gray, almost black. It is fairly well preserved and while the appendages are missing, the body is complete. The tail is bent on itself as shown in the figure. Taking the length of the bent portion into account, the complete length is ca. 15.5 mm. The carapace is flat, evenly rounded, without a trace of eyes, wider than long; but correct measurements are difficult. The tergites of the preabdomen are fairly equally long, except for the fourth one which is distinctly longer, though slightly narrower than the third. The lateral limits of the tergites are well visible. On the second and third postabdominal segments a pair of longitudinal crests are well visible. Superimpressed over the dorsal surface, portions of the ventral surface may be made out in illumination with slanting rays. One can see a pentagonal sternum against which the fourth coxae abut, and behind it a pair of narrow and long combs with numerous teeth. The third coxae are also visible, but of the second and first pair only indistinct indications are present. The sternum is pressed somewhat sideways and so turned that its left rear corner lies in the middle line. The angle between the combs is about 90°. Compared with the abdomen, the carapace is very small. The specimen produces the impression that it is a mature female of small size, because the pleura on the sides of the preabdomen is fairly wide, as if the abdomen were distended by eggs. In this respect it resembles *Lichnoscorpis minutus* shown in Figure 145, from which, however, it is easily distinguished by the absence of eyes and the shape of the abdominal tergites.

Genus *Typhlopisthacanthus*, new

Type *T. mazonensis* (Petrunkevitch), sub *Palaeopisthacanthus*

This genus is characterized by the unusual size of the carapace which is longer than wide, flat and devoid of eyes; and by the extremely short and slender tail. The latter character it shares with

the Genus *Palaeopisthacanthus* to which the type of the new Genus *Typhlopisthacanthus* was referred by me in 1913. However, the type of the former differs from the type of *Typhlopisthacanthus* not only by the presence of eyes, but also by the shape and proportions of its carapace. Figures of *T. mazonensis* (sub *Palaeopisthacanthus*) may be found in my Monograph (93) on page 50. A comparison of Figure 13 of that Monograph with Figure 143 of the present paper will show at a glance the congeneric affiliation of the British and American species. The two species may be separated by the following characters:

- a. Size 23 mm. Carapace distinctly narrowed in front. Tail about as long as the fifth preabdominal tergite. *T. mazonensis*.
- b. Size 10 mm. Carapace much less narrowed in front and with rounded anterior edge. Tail as long as at least the last three preabdominal tergites. *T. anglicus*.

Typhlopisthacanthus mazonensis (Petrunkévitch) sub *Palaeopisthacanthus*, Trans. Conn. Acad., 1913, Vol. 18, p. 50, Figs. 13, 14, Plate II, Fig. 1.

The type and only specimen No. 37977 from Mazon Creek, Illinois, is in the collection of the U. S. National Museum.

Typhlopisthacanthus anglicus n. sp. Figures 143 and 182.

Type. Specimen No. 31261 of the British Museum (marked also as No. 42) from the Upper Carboniferous of Coseley, Staffs. Two pieces, both showing the dorsal surface, but the one the reverse of the other. Figure 143 was made to show the specimen as it appears on that piece on which it is concave, but the missing portions of the tail are indicated by the dotted lines. The same piece is shown photographically in Figure 182. It is a very small scorpion, its length being approximately 10 mm. Exact measurement is impossible, because the abdomen is bent at a considerable angle and the tail twisted and partly missing. The carapace is flat and smooth, 3.6 mm. long, 3.0 mm. wide, with almost parallel sides and evenly rounded anterior end. Compared with its American relative it is a considerably smaller species with a carapace distinctly less narrowed in front. The postabdominal segments seem to be somewhat longer than in the latter, but the preabdominal tergites, except for the effect of distortion, increase similarly in length from the anterior to the posterior end.

Genus *Typhloscorpius*, newType *T. distinctus*, n. sp.

This genus is established on the basis of the carapace alone, as that is the only portion of the scorpion in existence. Fortunately, notwithstanding slight distortion it is excellently preserved.

Typhloscorpius distinctus, n. sp. (Figures 146, 178)

Type. Specimen In. 13909 of the British Museum, from the Coal Measures of Coseley, represented by two pieces, both showing only the carapace, the one being the cast of the other and therefore, except for slight distortion of its left side looking like the original. It is shown in Figure 146 and photographically in Figure 178. Although in many respects resembling specimen No. 39772 (*Lichnophthalmus pulcher*) shown in Figures 139 and 177, it is distinct from it because it *has no eyes*. The pair of protuberances shown in Figure 146 as little black dots with three lines radiating from them, are definitely not eyes, but rather sharply pointed elevations, very different from anything that could be confused with eyes. The carapace is 7.9 mm long and 9.1 mm. wide, if one simply doubles the measurement taken of the right half at the posterior margin, the left half being somewhat bent downward and evidently out of shape. The anterior edge is distinctly convex in the middle, slightly concave toward the anterior corners, convex here only to become again distinctly concave on the sides all the way to the posterior corners. The cephalic portion is strongly elevated and has very steep sides. It extends almost to the posterior edge of the carapace, which is strongly margined and distinctly thickened. Beginning at the anterior margin on each side half way between the middle point and the lateral corner, two deep sulci run backward in a slight curve, gradually merging at a point approximately in the middle of the carapace. From here on the single median sulcus extends to the posterior end of the cephalic portion. A short anterior median sulcus runs from the anterior median point backward, only to disappear in a low plateau behind the pair of pointed tubercles mentioned above. The outer edge of the converging sulci is accompanied by irregularly arranged granules which extend also on each side of the posterior median sulcus almost to its end. This description of the carapace is based on the study of that piece which represents the cast and corresponds therefore to the actual structure as it was in life. The piece representing the mold is naturally the negative of the former.

Assuming the relative proportions of the body of the common, now living, European scorpion *Eoscorpio italicus* as fairly representative of scorpions in general and finding that its carapace is from six and a half to seven times shorter than the total length, we arrive at the approximate length of *Typhloscorpins distinctus* as being between 51 and 55 mm., i.e. appreciably greater.

Genus *Lichnophthalmus*, new

Type *L. pulcher* n. sp.

This genus is also based only on the structure of the carapace, that being the only part preserved. The carapace resembles that of *Typhloscorpins*, but has an eye-tubercle with a pair of ellipsoidal eyes.

Lichnophthalmus pulcher n. sp.

Type. Specimen In. 39772 from the Middle Coal Measures, Crow Coal, Phoenix Brickworks at Crawcrook near Ryton-on-Tyne, Durham, collected and presented by Wm. Eltringham, July 1940. British Museum. It is represented by a single piece which corresponds to a cast and shows all structures as they were in life. The color of the specimen is the same as that of the matrix, dark grey-brown. The specimen is shown in Figure 139 and photographically in Figure 177.

The left side of the specimen is fully exposed and complete; on the right side the cephalic portion is complete, but the flat thoracic field is missing. The carapace is 11.0 mm. long, 13.7 mm. wide if one figures the width by doubling the distance between the median line and the left edge. The cephalic portion is elevated, but not nearly as much as in *Typhloscorpins* and its sides are not steep. The anterior edge has the same shape as in the latter and the cephalic portion extends similarly almost to the posterior margin which is thickened. But the sides are more converging anteriorly. In place of the anterior median sulcus and paired tubercles there is a well defined eye-tubercle, the long axis of which is transverse. The two eyes are perfectly preserved. They are not round, but ellipsoidal, the two long axes forming between them an angle of about 90°. They are separated from each other by 0.43 mm., and the long and short axes of each eye are 1.57 and 1.29 mm. There are very distinct round granules on the carapace, forming two, more or less strongly converging rows. Applying to the specimen the same ratio of measurements as used above, we find that the total length of the specimen must have been between 71 and 77 mm.

On the left side of the carapace, on the level of the median eyes there is a short, but distinct ridge visible even in the photograph and reminiscent of that often associated with the lateral eyes in Recent scorpions. However, careful examination failed to show imprints of eyes, and the ridge itself is wanting on the right side. Without being able to reach a definite decision in this regard, I think that the probability is in favor of the assumption that the species had no lateral eyes.

Genus *Lichnoscorpius*, new

Type *L. minutus* n. sp.

This genus could be confused with *Anthracoscorpio* but for the presence of eyes on the carapace and the shortness of the anterior abdominal tergites. Unfortunately the combs are not preserved and this character cannot be used for comparison and differentiation.

Lichnoscorpius minutus n. sp.

Type. Specimen In. 31266, represented by two pieces, both showing the dorsal surface without any traces of the ventral one. The piece corresponding to a cast is not as well preserved, nor as complete as the piece representing the mold. The latter is shown in Figure 145 and photographically in Figure 181. The specimen was collected by Mr. W. Eddington who presented it to the Museum. It is also marked as No. 50 and comes from the Upper Carboniferous Coal Measures of Coseley.

The specific name was selected to emphasize the small size of the species, for it seems to be a mature specimen, judging by the distended shape of its abdomen, presumably a female. Total length approximately 9.0 mm., carapace 1.41 mm. long, 1.71 mm. wide, almost semi-circular in appearance, flat, with a ridge between the perfectly round eyes (Figure 144) which are separated by their diameter and by approximately one and a half diameters from the anterior edge of the carapace. The eyes are visible only on the piece representing the mold and they and the interocular ridge appear therefore as depressions, but with perfectly sharp outlines. There is no eye-tubercle, the level of the eye-circumference being the same as that of the carapace. The abdomen is considerably wider in the middle than the posterior edge of the carapace. The tergites increase in length from the first to the seventh. The tail is composed of

segments which are as wide as long and have a pair of longitudinal ridges, except for the fifth one which has a single ridge.

Genus *Compsoscorpius*, new

Type *C. elegans*, n. sp.

This genus is characterized by the shape of its carapace which is more or less parabolic and not semicircular, and sculptured; by the elongated eye-tubercle, the long axis of which coincides with the axis of the body; by the circular shape of its median eyes; by the presence of three pairs of small, lateral circular eyes situated a little in advance of the median ones; and by the elongated shape of the hand and fingers. Two species belong to this genus, *C. elegans* which is the Genotype, and *C. elongatus*, both from the Upper Carboniferous of Coseley.

Compsoscorpius elegans n. sp.

Type. Specimen In. 7883, from the bed of nodular ironstone, about 10 feet above the thick or 10 yard coal, Coal Measures, Coseley, Staffs, W. Madeley Coll. Two pieces, both showing only the dorsal surface, one as a cast, the other, better and more complete one, as a mold.

This is the specimen which Pocock (111) identified as *Anthracoscorpio buthiformis*, described on page 26 and shown in Fig. 7. The specimen, when examined by me, looked exactly like Pocock's figure. After careful cleaning it was possible not only to expose the entire carapace with its median and lateral eyes, but one preabdominal tergite in front of those shown by Pocock and three postabdominal segments previously concealed deeply under the surface of the matrix.

The specimen, as it appears now, is shown in Figure 151 which represents the mold, while Pocock's figure was made from the cast, and Figures 152-154. The specimen is shown also photographically in Figures 183 to 185. Of the appendages only the two pedipalps are preserved, but both are complete. Portion of the femur of the first right and the complete femur with a piece of the patella of the second right leg are also preserved. Of the preabdomen the anterior two tergites are missing, of the postabdomen the posterior two segments and the poison-gland are also missing. Assuming the length of the missing tergites to be equal to one and a half of the length of the fourth tergite and the length of the missing portion of the postabdomen to equal the length of the preserved portion, we can estimate the total length of the specimen as ca. 17 mm. with

a tail distinctly longer than the preabdomen. The carapace is 2.57 mm. long, 3.43 mm. wide (Pocock gives its width as 3.5 mm. I think that this discrepancy may be easily explained by the greater perfection of the measuring instruments which I used). The hand is 5.0 mm. long and 1.14 mm. wide. The fingers are distinctly curved. The femur with the patella are somewhat shorter than the hand and not longer, as given by Pocock. The carapace is margined behind and on both sides and shows more or less radiating ridges with depressions between them. The posterior end of the cephalic portion is about two-thirds of the length of the carapace from its anterior edge. The eye-tubercle is neatly ellipsoidal and the median eyes when viewed from above appear to be elliptic. However, when one looks at a median eye at an angle to the surface of the carapace, such that the line of vision would coincide with the vertical axis of the eye, the latter appears perfectly circular, as shown in Figure 153 and photographically in Figure 185. The lateral eyes are plainly visible when the surface of the specimen is greatly inclined. They, too, are perfectly circular, separated from each other by about their diameter and arranged in a slightly curved line as shown in Figure 154. It is almost impossible to show them clearly on a photograph, because of their small size requiring high magnification. Their position on the carapace is marked by a curved, elevated ridge to the inside of which they are situated.

Compsoscorpius elongatus n. sp.

Type. Specimen In. 15862 represented by two pieces from the Upper Carboniferous Coal Measures of Coseley, Staffs. Both pieces show only the dorsal surface, one as a mold, the other as a cast; the carapace is better preserved in the former, the abdomen and tail in the latter, but both are visible on both pieces. Figure 147 was made from the piece representing the cast, Figures 148-150 from that showing the mold. The corresponding photographs appear in Figures 186-188. The carapace is distorted and thanks to this distortion it was possible to incline it so as to photograph the small, lateral eyes (Figure 188). Like the carapace of the genotype the carapace of *C. elongatus* is more or less elongated, but with stronger converging sides, while the posterior edge is straight, as in the genotype. The carapace is margined all around, clearly sculptured and with distinct small punctures (granules in life) on its surface and on its margins. In the median line is a well defined crest (groove in life) extending from

the anterior end of the eye-tubercle to the posterior margin of the carapace. The eye-tubercle is ellipsoidal, the median eyes circular, but much farther apart than in the genotype. They are of the same size as those of the genotype, but the lateral eyes are distinctly larger than the corresponding eyes of the genotype. The eye-tubercle is complete, but the right side of the specimen is greatly distorted. Measurements of the width are therefore possible only as the double of the distance from the left side to the middle. The tail is turned sideways, with only its left side visible. Of the appendages only a few pieces are left and these cannot be referred to the proper pair.

Total length 29.42 mm. Carapace 4.14 mm. long, 5.14 mm. wide. Preabdomen 10.71 mm. long, 4.29 mm. wide across the fifth tergite. First tergite 0.86 mm. long, sixth tergite 2.14 mm. long. Postabdomen including poison-gland 14.57 mm. long; first segment 1.86 mm. long, 2.14 mm. wide; fifth segment 4.29 mm. long, 1.86 mm. wide. Lateral longitudinal crests are present on all segments of the postabdomen, the dorsal crest of the second and third segments studded with a row of granules. Superimposed on the first tergite of the cast piece dim outlines of the combs may be made out.

The two species of *Compsoscorpius* may be distinguished as follows:

a. Size smaller, ca. 17 mm. Carapace with convex sides. Median eyes separated from each other by one third of their diameter. *C. elegans*.

b. Size larger, ca. 30 mm. Sides of carapace straight, converging. Median eyes separated by their diameter. *C. elongatus*.

Genus *Eoscorpius* Meek and Worthen, 1868

Type *E. carbonarius* M. a W.

The characters of the genus as given in the key are different from those used by me in 1913. Of the eight species listed under this genus then, *E. ornatus* (Fritsch) cannot be affiliated with any known genus on account of lack of important, distinctive characters; *E. danielsi* and *E. granulatus*, having a carapace much wider than long, are here placed in the new Genus *Alloscorpius*. This leaves in the Genus *Eoscorpius* only five species, three of them European, *E. buthiformis*, *E. dunlopi* and *E. sparthensis*, and two North American, *E. carbonarius* and *E. typicus*. All specimens examined by me and those for which measurements and descriptions are given by Pocock, conform with the genotype in proportions and structure of their carapace. The only

exception is the specimen which Pocock described as *Anthracoscorpio buthiformis* from Mr. Madeley's collection and which now becomes the genotype of the new Genus *Compsoscorpins* (q.v.). As delimited here the Genus *Eoscorpins* is very uniform.

Key to Species of *Eoscorpins*

(The distinctive characters of the British species are taken from Pocock's descriptions of them.)

1. Carapace subrectangular, about as long as wide 2
- Carapace distinctly narrower in front, and longer than wide 3
2. Sixth abdominal tergite wider than the first. Size about 90 mm. *E. carbonarius*.
- First abdominal tergite wider than the sixth. Size from 45 to 65 mm. *E. typicus*.
3. Size 130 mm. First four segments of the tail together two and a half times longer than the carapace. Width of hand less than one-third the length of the movable finger. *E. dunlopi*.
- Size not over 75 mm. First four segments of the tail only twice as long as the carapace 4
4. Size ca. 75 mm. Width of hand equals about one-half the length of the movable finger. *E. sparthensis*.
- Size ca. 22 mm. Hand just a little longer than carapace. Dorsal integument granular. *E. buthiformis*.

Eoscorpins carbonarius Meek and Worthen, Amer. Journal of Sci. a Arts, (2) 1868, Vol. XLV, p. 25. Petrunkevitch, Trans. Conn. Acad., 1913, Vol. 18, p. 37, Plate II, fig. 6.

A single specimen, the type, from Mazon Creek, Illinois.

Eoscorpins typicus Petrunkevitch, Trans. Conn. Acad., 1913, Vol. 18, p. 39, Text-figures 5-7, Plate I, figs. 1-4.

Type, No. 37986, in the U. S. National Museum, Specimen No. 37987 also there. Specimens No. 126 and 127 in Peabody Museum of Yale University. All from Mazon Creek, Illinois.

Eoscorpins sparthensis Baldwin & Sutcliffe, Quart. Journal Geol. Sci. 1904, Vol. LX, p. 396, fig. 2.

One specimen, Type, from the Middle Coal Measures of Sparth

Bottom, near Rochdale in Lancashire. Another specimen in the British Museum from the Coal Measures of Bohemia.

Eoscorpius dunlopi (Pocock) sub *Anthracoscorpio*, Terrestrial Carboniferous Arachnida, 1911, p. 21, Text-figure 5, Plate I, fig. 1.

A single specimen, the type, from the Upper Coal Measures of Drumgray, Scotland.

Eoscorpius buthiformis (Pocock) sub *Anthracoscorpio*, Ibid., p. 24, Text-figures 6 and 8 (not 7), Plate II, fig. 1.

Type from the Coal Measures of Sparth, near Rochdale. Five other specimens from the Dudley Coalfield (according to Pocock).

Eoscorpius inflatus Peach (91) was proposed for a very imperfectly preserved specimen showing only a distorted carapace. Peach himself was at first tempted to place it in a genus without designation of any order to which it may belong. Pocock agreed with that idea insofar as he believed it impossible to assign definitely to any arachnid order.

Genus *Alloscorpius*, new

Type *A. granulatus* (Petrunkévitch) sub *Eoscorpius*.

The two species belonging to this new genus were originally placed by me in the Genus *Eoscorpius*. The resemblance with the representatives of the latter genus is great, but the distinctive characters seem to me to be of sufficient importance to require the erection of the new genus for their reception. For whereas in the species to which the Genus *Eoscorpius* is restricted here, the carapace is either as long as wide or longer than wide, in both species of *Alloscorpius* it is distinctly wider than long. The position of the eyes is also different. In *Alloscorpius* they are much nearer the anterior edge of the carapace than in *Eoscorpius*. The two species may be distinguished as follows:

- a. Abdominal tergites each with a transverse row of granules along the posterior edge. *A. granulatus*.
- b. Abdominal tergites smooth. *A. danielsi*.

Alloscorpius granulatus (Petrunkévitch) sub *Eoscorpius*, Trans. Conn. Acad., 1913, Vol. 18, p. 45, Text-figure 9, Plate II, fig. 10, Plate III, figs. 11, 12. Three specimens including the type, from Mazon Creek, Illinois, in the Peabody Museum of Yale University.

Alloscorpius danielsi (Petrunkévitch) sub *Eoscorpius*, Trans. Conn. Acad., 1913, Vol. 18, p. 43, Text-figure 8, Plate IV, fig. 16. A single specimen from Mazon Creek, Illinois.

Genus *Palaeopisthacanthus* Petrunkevitch, 1913, emendedType *P. schucherti* Petrunkevitch

As emended here this genus is now reduced to a single species, the genotype, characterized by the proportions and size of the carapace, and by the possession of a pair of eyes.

Palaeopisthacanthus schucherti Petrunkevitch

Trans. Conn. Acad., 1913, Vol. 18, p. 48, Text-figures 11, 12, Plate II, figs. 8, 9. A single specimen, the type, No. 140, from Mazon Creek, Illinois, in Peabody Museum of Yale University.

Genus *Europhthalmus*, newType *E. longimanus* n. sp.

The characters of the genus are given in the key. They are derived from the proportions, shape and structure of the carapace and the unusual length of the pedipalp.

Europhthalmus longimanus n. sp.

Type. Specimen In. 39766 from the Middle Coal Measures, Crow Coal, Phoenix Brickworks at Crawcrook near Ryton-on-Tyne, Durham. Collected by Wm. Eltringham, July 1940. Two pieces, both showing only the dorsal surface with a carapace and the first abdominal tergite of another specimen superimpressed on both pieces over the middle of the preabdomen at right angles to its longitudinal axis. This portion possibly belonging to an unknown genus with a rather large, rectangular and apparently blind carapace, is not shown in our figures. At present it cannot be identified. Portions of the tergites of the type itself are somewhat disrupted. The photograph No. 174 shows the specimen in natural size. Figure 140 shows it with omission of the foreign carapace and with the tergites restored in their proper place. Figure 141 shows the complete hand as it appears on the other piece.

Total length ca. 60 mm. Carapace about 10.5 mm. long, its width impossible to measure exactly. The eyes are large and round, separated by what must have been a sulcus, for they appear as concave and the space between them as a ridge. The eyes are very close to the anterior, evenly rounded edge of the carapace and are separated from each other by their diameter. The surface of the carapace is uneven and covered with coarse punctures showing that in life it was roughly granular. The abdominal tergites increase in length in accordance with their

sequence, the third tergite being half as long as the seventh. The first three segments of the postabdomen are short, the second slightly wider than long, the fourth not quite twice as long as wide, and the fifth twice as long as the third. This segment and the poison-gland are turned sideways and the fifth segment shows a dorsal projection near its posterior end, representing probably a pointed tubercle. Of the appendages only the right pedipalp is complete. Its femur shows a fold near its anterior end, which gives it the appearance of a supernumerary segment. This, of course, is not so. It is due to injury, in the process of fossilization. The femur is even so shorter than the patella. The measurements are as follows: femur 10.3, patella 10.7, tibia to end of finger 18.7, (to base of movable finger 8.0). Movable finger 10.7 mm.

Europhthalmus sp?

I place provisionally and only tentatively under the Genus *Europhthalmus* the single segment of a scorpion's tail found in the Middle Coal Measures in shale over Barnsley thick coal, in the Monckton Main Colliery near Barnsley, Yorkshire in 1894 by W. Hemingway. The specimen consisting of two pieces mounted on a single board has the invoice number of the British Museum 18603 with an accompanying statement by Dr. Calman in answer to a query from Dr. Bather, which reads: "I don't think this can belong to any Crustacean or Arachnid known to me." (dated 3.IX.19). I think that a comparison with numerous fossil scorpions warrants my assumption that the specimen in question is a segment of a scorpion's tail still showing the anterior portion which is normally hidden inside the preceding segment, the completely exposed and normally the only visible portion of the segment, the sculpturing of its wall and the granules along its edges (Figures 142 and 179). The longitudinal median crest divides the segment so symmetrically into two portions each of which is almost a mirror image of the other, that the further assumption seems to be warranted, that the segment presents its dorsal surface. The length of the exposed portion is 8.4 mm., its width 7.2 mm. Its superficial resemblance to the tail-segments of the Middle Coal Measures species *E. longimanus* suggests that the segment in question may belong to another species of the same genus. If so, and if the proportions of that species were similar to those of *E. longimanus*, then it may be regarded as being the second, or third segment. The measurements of the third segment of *E. longimanus* are: length - 2.8, width 2.2 mm. The

segment in question is three times longer, indicating that the species was about 180 mm. long, i.e. of approximately the same size as the Recent *Palamnaeus* (*Heterometrus*) *swammerdami* from India, which reaches 176 mm., and *Pandinus imperator* of West Africa, which attains fully 180 mm. in length. They are the largest now living species.

In the collection of the British Museum, which forms the basis of the present investigation, there are also two specimens of tail-segments of scorpions from the Upper Carboniferous Coal Measures of Coseley, Staffs. The specimen In. 7890, represented by two very well preserved pieces, consists of three connected segments. The medium of these is 6.6 mm. long, 5.4 mm. wide, this would give the total length of the scorpion as about 140 mm., i.e. approximately that of the Recent *Palamnaeus indus* and *P. phipsoni* of India.

The specimen In. 1566 consists also of two pieces, both showing two complete, connected tail-segments and a small portion of what I assume to be the poison-gland. The segments resemble the fourth and fifth segments of *Compsoscorpius elongatus*. The fourth is square, 2.8 by 2.8 mm., the fifth is 5.0 mm. long and 2.8 mm. wide. This would mean that the total length of the scorpion to which the piece in question belonged was only a little greater than that of the type of *C. elongatus*.

2. Order PSEUDOSCORPIONES (Chelonethi)

There are no representatives of this order in the Palaeozoic. Whether their absence is due to their belated evolution from the arachnid stem or to the simple fact that as yet they have not been found; cannot be decided at present. Their small size makes collecting of living species difficult unless one employs special instruments and methods. If their size was the same in the Palaeozoic as at present, the fact that no fossil records earlier than the Coenozoic exist may be easily accounted for.

For the convenience of students of fossil Arachnida the Order is included in the key and the disposition of the coxae is shown in Figure 6. The following references dealing with the structure of pseudoscorpions and with the classification of Recent species may be given here. 1. J. C. Chamberlin. The Arachnid Order Chelonethida. Stanford University Publications. Biological Sciences. Volume VII, No. 1. 1931. 284 pages. Numerous text-figures. Bibliography.

2. C. Fr. Roewer. Chelonethi. Bronns Klassen und Ordnungen des

Tierreichs. Fifth volume, fourth section, sixth book. Leipzig, 1936-1937. 320 pages.

3. Max Vachon. Recherches anatomiques et biologiques sur la reproduction et le développement des Pseudoscorpions. Thèse Fac. Sci. Paris, 1938. Ser. A. No. 1779, 208 pages.

3. Order OPILIONES

The Order Opiliones is rich in Recent species exhibiting a variety of structure. Nevertheless it is a fairly uniform order when examined from the point of view of distinctive characters. For those who wish to get acquainted with the structure of opilionids and with their classification, the following three references may be helpful.

1. H. J. Hansan and W. Sørensen. On Two Orders of Arachnida. Cambridge University Press, 1904. Opiliones. pp. 1-113. Pls. 1-6.

2. Alfred Kästner. Opiliones. Kükenthal's Handbuch der Zoologie, third volume, second half. Pages 300-393, 1935-1937.

3. C. Fr. Roewer, Die Weberknechte der Erde. Jena. 1923. 1116 pages.

The ventral surface of three representatives of the Order are shown in our Figures 9, 10 and 11. They give an idea of what may be regarded as extremes of modifications in Recent species.

Only four species have been described from the Palaeozoic. *Nemastomoides elaveris* Thevenin, judging by the published figures of the Type, from the Coal Measures of Commeny, France, probably is an opilionid. The specimen from Scotland described and figured by Pocock as *N. elaveris* looks more like a member of the Order Trigonotarbi. Fritsch's *Dinopilio gigas* as figured on his Plate 5 and in Text-figure 35 on page 30, shows no characters typical of opilionids. *Protopilio longipes* and *P. depressus* described and figured by me in 1913 from the Pennsylvanian of Mazon Creek show a distinct resemblance to Cyphophthalmids, although "they are far from being typical Opilionids." (p.110). There seem to be no newer records of Palaeozoic opilionids.

The characters of the order, sufficient for the recognition of fossils, are given in the key. The most noticeable trend in Recent species is the fusion of anterior abdominal segments with the cephalothorax and the coincident displacement of the genital opening forward. Per-

haps it is correlated with the presence of a single, long penis in the male and a single, long ovipositor in the female. Their nervous system is characterized by the concentration of all existing neuromeres in the thorax, with a complete loss of at least eight neuromeres of the normal number of twelve, which one would expect to represent the ancestral number of all Arachnida. Only median eyes are present. A strainer is lacking in the foregut, resulting in an inability to prevent coarser particles from entering the midgut. Organs of respiration are represented only by tracheae with a single pair of spiracles situated on the abdomen behind the coxae of the fourth pair of legs. The coxal glands open by a single outlet on each side of the body at the base of the coxae of the third pair of legs.

4. Order ARCHITARBI

Introductory Remarks.

In my paper on the Palaeozoic Arachnida of Illinois (101) I gave a detailed account of the Order Architarbi and a key to its families and genera. The reasons for changing the name of the order from Phalangiotarbi to Architarbi were also given there in detail. Briefly, they may be condensed to the statement that the Genus *Phalangiotarbus*, with its single species based on the description of the better of two very incomplete specimens, is the least known among all the genera belonging to this order, whereas the Genus *Architarbus* is not only well known, but antedates the Genus *Phalangiotarbus* by twenty-two years. More recently I had the opportunity to study a specimen of *Phalangiotarbus subovalis*, the existence of which had been completely overlooked by Pocock and all the other investigators, myself included. An account of that study has been now completed and is published elsewhere, accompanied by figures of the specimen (104 b). The evidence is presented there that *Phalangiotarbus subovalis* is a typical architarbid and that the Family *Phalangiotarbitidae* is a synonym of *Architarbitidae*. This makes the use of the name Architarbi not only preferable to that of Phalangiotarbi, but imperative and fortunate. In the present paper the Family *Phalangiotarbitidae* is therefore omitted, but the Genus *Phalangiotarbus* is retained and is included in the key to genera of *Architarbitidae*.

In 1945 (101) I proposed several new genera, referred Pocock's *Geraphrynus torpedo* to the Genus *Leptotarbus*, suggested that his *G. angulatus*, *G. hindi* and *G. tuberculatus* belong to the Genus *Para*

tarbus, and *G. angustus* possibly to the Genus *Hadrachne*. The difficulty in placing species into genera solely on the basis of published descriptions and figures is rooted in the inadequacy of available data and in the impossibility of verifying them without access to the type specimens and without permission to subject the latter to thorough cleaning for the purpose of exposing to view structures which escaped the observation of the original investigator. Thus my own study of American species of *Architarbi* has convinced me that whenever an eye-tubercle is present, it has three pairs of eyes, while in species with a single pair of eyes the eyes are sessile, i.e. their periphery is on a level with the surface of the carapace itself, there being no eye-tubercle present. Now, in describing the British species *Gera-phrynus angulatus* Pocock states: "median eyes distinct and placed apparently on a tubercle which has a convex anterior border." He figures two eyes and a line or two, indicating the presence of a tubercle without mentioning either of them, in *G. tuberculatus* and *G. eggintoni*. Consequently if his statement and figures are correct, then these three species differ not only from the American *Architarbi* with an eye-tubercle, but, as we shall see below, from British specimens which were sent to me for study by the British Museum and which have three pairs of eyes on their eye-tubercle. Yet these latter specimens most likely belong to Pocock's species. Presumably Pocock did not see the other two pairs of eyes because the specimen was not sufficiently cleaned to show them. Under the circumstances it is impossible to decide whether the specimens described below belong to a new species or to Pocock's species, because they differ from the latter only by their eyes, and that difference, unfortunately, happens to be of generic value. To avoid further confusion and undesirable duplication of names I decided to give the same name *tuberculatus* to the species described below as new and to place it in a new genus. If some day in the future somebody will be fortunate enough to re-examine Pocock's type specimen and should the reexamination prove the presence of three pairs of eyes (not of only two eyes, as Pocock states), then my specimens and with them my new species will become synonyms of Pocock's species *without a change of their specific name*. The new genus will, of course, remain, because it is based on characters necessitating its erection.

As already explained in the Introduction, the present study required careful comparison of the structure of the mouth parts and of the position of the mouth in all orders of Recent Arachnida. The arrange-

ment of the coxae in *Architarbi* resembles most that of the *Cyphophthalmi* among the *Opiliones*. This fact was noticed many years ago, but the inference from it escaped all previous investigators, myself included. I was even led to believe that in species, in which the pedipalpal coxae are altogether not visible, they are permanently fused with the coxae of the first pair of legs, appearing now as medial processes without any trace of their original nature. Even in my paper published in 1945 I still believed it to be the case and used this character in the key to the genera for distinction from such, in which the pedipalpal coxae are separate and wedged in between the first pedal coxae. I am firmly convinced now that this difference is quite irrelevant and perhaps even due merely to the state in which the specimens became fossilized. But to make this point clear, we must first consider the structure of the ventral surface in *Cyphophthalmi* and its relation to the position of the mouth and to the so-called stomotheca.

The coxae of each side in *Cyphophthalmi* are contiguous, the first pair is movable, the second pair varies in this respect, the third pair is coalesced with the fourth and immovable in all species. According to Hansen and Sørensen (39) "the first coxa is in all *Cyphophthalmi* capable of a little movement whereby its maxillary lobe can be brought near to or away from the mouth." (p.27). This arrangement of the coxae stands in direct relationship to the structure of the stomotheca. The latter was first studied by Thorell. Hansen and Sørensen discussed it in detail and gave an excellent account of its structure. According to them an underlip or labium is wanting. "The mouth is placed in a cup-shaped depression to which Thorell gave the name of stomotheca, which we adopt. The stomotheca is formed by the first pair of coxae, but is closed behind by the maxillary lobes of the coxae of the second pair of legs. The inner surface of the first pair of coxae forms always the side walls, and in some genera, viz. *Pettalus*, *Purcellia*, *Siro* and *Parasiro*, these surfaces also partly close it above. It is not, however, the entire inner (or anterior) surface of the first pair of coxae that enters into the composition of the stomotheca, but only the proximal portion, which as a rule is the longer one, while the distal portion slants inwards and forwards, forming a more or less sharp corner with the proximal part. The under surface of the coxa makes an angle with the proximal portion of the inner surface, which forms the wall of stomotheca, but rounds off more gradually into the distal portion of the same, which is situated in front of stomotheca.

On the under surface of the first coxa a ridge runs along the border of stomotheca, our carina stomothecae, which is marked off by a groove, and of which the anterior extremity often forms a projecting point. Thorell has already drawn attention to the fact that the shape of stomotheca is different in different genera." (p. 31). An upper lip or labrum is always present in front of the mouth in all Cyphophthalmi. "Labrum proper is rather broad just at the base, but the larger, anterior, distal portion, which extends forward between the anterior portion of the mandibles, is so much compressed from the sides that as a rule it is difficult or even impossible to see it on account of its narrowness, except by dissection." (p.34). It will be seen from this description that the mouth opens in Cyphophthalmi ventralward, but is situated *above* the ventral surface of the coxae, because it is separated from the latter by the cavity of the stomotheca. It must be also kept in mind that the mouth is flanked on the sides by the pedipalpal coxae, (*mandibles* in the terminology of Hansen and Sørensen, *maxillae* in the terminology of most other authors at present), and that the latter are wedged in between the first coxae and dorsal to the ventral surface of the latter. (Figure 11). To get an arrangement comparable with that in Architarbi (Figure 12), it would require only a greater lateral extension of the first coxae toward the median line. This would bring them in contact with each other along the median line and thus hide from view completely the pedipalpal coxae, the labrum and the mouth. If the first coxae remained independent and movable at least to some extent, access to the stomotheca, and therefore to the mouth as well, would be provided in the shape of a narrow slit when the coxae would be moved apart. Then one could get a view of the pedipalpal coxae in the wedge-like slit between the first coxae. In a fossil they would of course appear more or less in the same plane, just as they do in many American species. In reality they would be *above* the first coxae. The fact that one never sees five joints in the palp of the Architarbi is a confirmation of the interpretation as given here. For if the coxae of the pedipalpi had fused with the first pedal coxae, the normal number of joints should be visible at least in some specimens.

Characters of the Order

Fossil Arachnida with broad juncture between the cephalothorax and the abdomen. Carapace entire, either with a pair of sessile eyes or with three pairs of eyes on a trifoliate eye-tubercle, or completely

devoid of eyes. Ventral surface of cephalothorax occupied entirely by the four pairs of pedal coxae and a narrow, elongated sternum. All coxae of the same side contiguous, those of the first pair alone presumably movable. Sternum usually composed of three sclerites. Lower lip or labium wanting. Pedipalpal coxae (maxillae) situated *above* the first pedal coxae and visible only when the latter are moved apart. A stomotheca is probably formed by the sides of the first coxae as in *Cyphophthalmi*, but concealed from view. Chelicerae three-jointed, chelate. Pedipalpi six-jointed, pediform, slender, partly concealed by the first coxae. Only the first coxae with gnathites (maxillary processes), the other coxae without them. Trochanters single-jointed except in one family in which the third and fourth pair of legs have two-jointed trochanters. Abdomen segmented, with from ten to eleven tergites, the anterior four, five or six of which are greatly abbreviated and longitudinally divided by a fine, median line. The number of sternites usually smaller than that of the tergites, the most frequented number being nine. The sternites are always divided into three fields by a pair of longitudinal lines. The pleural membrane connecting the tergites with the sternites on each side of the body is soft and unsegmented. Anus ventral, on the last sternite, with an operculum, which is round and consists of a single valve, but occasionally shows its origin from a pair of constituent elements by the presence of a median longitudinal line in its anterior half. Respiration supposedly by means of ventral sacs situated on the third to sixth sternites. First abdominal sternite triangular, bordered on the sides by the fourth coxae. A pair of openings on the second sternite, presumably of seminal receptacles. A dorsal, elongated heart with three posterior arteries present at least in one specimen (*Orthotarbus robustus* No. 14878 of the Illinois State Museum).

Key to Families of Architarbi

1. First pair of legs thin and long. Coxae of first pair of legs completely separated by the pedipalpal coxae and in their turn separating the coxae of the second pair. Third and fourth coxae long, with parallel sides, contiguous, each pair meeting with its proximal ends in the median line. Ten tergites, the first five abbreviated. Sternites not known. Family *Heterotarbidæ*.
- All legs similar, more or less stout. All coxae triangular, contiguous. Pedipalpal coxae either completely hidden by the

- first pedal coxae, or else partly visible as narrow wedges and never completely exposed to view 2
2. Trochanters of third and fourth pair of legs two-jointed. Abdomen with eleven tergites, the first six abbreviated. Family *Opiliotarbidæ*.
- All trochanters single-jointed. Abdomen with ten tergites and at least eight, usually nine sternites. Family *Architarbidæ*.

1. Family ARCHITARBIDÆ Karsch, 1882

This family which is typical of the order is readily recognizable by the characters given in the key. The carapace is of variable shape, with either a pair of sessile eyes, or with three pairs of eyes on a trifoliate eye-tubercle, or without eyes. The abbreviated tergites are divided by a median line, but their shape varies, determined by the shape of the posterior edge of the carapace. The third to penultimate sternites are always divided into three fields each by a pair of longitudinal lines.

In my paper of 1945 I divided this family into nine genera on the basis of the structure of the carapace. One of these genera, *Leptotarbus*, was proposed by me for a British species described and figured by Pocock and so distinct from the other genera, that the erection of a new genus seemed to be safe and advisable. The Family *Architarbidæ* is much better represented in America than in Europe. Besides the six British species described by Pocock in 1911, a single European species seems to have been discovered by Kliver in 1886, and placed by Waterlot in 1934 in the Genus *Opiliotarbus*, to which it most certainly does not belong. Waterlot's arguments in favor of his opinion are quite at variance with all principles accepted by arachnologists and followed in the classification of Recent Arachnida. Presumably it belongs into the Family *Architarbidæ*, but the description of the specimen is too incomplete and the figure too inadequate to permit its assignment to any one of the genera recognized by me. The species which Waterlot named *O. kliveri* may be recognized by the triangular shape of its carapace with a straight posterior edge and by the angulate shape of the two posterior intertergal lines. Fortunately Pocock gave a key for the separation of his six species and, by adding to it the specific characters of Waterlot's and my European species of *Architarbi* I found it possible to give a

key to *all* European species without assigning them to genera. This key, which will be found at the end of the chapter, will be, it is hoped, welcomed by students of European collections.

Key to Genera of Architarbidae

1. Carapace longer than wide, its posterior edge more or less strongly procurved. Anterior tergites also procurved. Pedipalpal coxae not visible, concealed by the contiguous coxae of the first pair of legs 2
- Carapace wider than long. Pedipalpal coxae visible 5
2. Carapace rhomboidal, its posterior edge sinuous, concave near its juncture with the lateral sides. A pair of sessile eyes present. Genus *Architarbus* Scudder.
- Posterior edge of carapace evenly rounded, procurved 3
3. Six eyes on a trifoliate tubercle present. Genus *Mesotarbus*, new.
- Eye-tubercle and eyes wanting 4
4. Carapace subtriangular, only a little longer than wide, with convex sides, acutely pointed in front. Genus *Hadrachne* Melander.
- Carapace much longer than wide, with gently converging sides which are almost straight in posterior two thirds, becoming distinctly curved in anterior third. Anterior point of carapace less acute. Genus *Leptotarbus* Petrunkevitch.
5. Carapace rectangular, with parallel sides, rounded anterior corners and straight posterior edge. Anterior edge with a small triangular projection in middle. Six eyes on a trifoliate tubercle present. Genus *Geratarbus* Scudder.
- Carapace with convex, converging sides 6
6. Carapace evenly rounded in front, six eyes on a trifoliate tubercle present. Genus *Ootarbus* Petrunkevitch.
- Carapace pointed anteriorly, with convex sides 7
7. Six eyes on a trifoliate tubercle present 8
- Either only a pair of sessile eyes or eyes wanting 9
8. Posterior edge of carapace straight. Genus *Orthotarbus* Petrunkevitch.
- Posterior edge procurved, angular. Genus *Goniotarbus*, new.

9. A pair of sessile eyes present. Genus *Paratarbus* Petrunkevitch.
 — Eyes wanting 10
10. Carapace subtriangular, flat. Six anterior tergites abbreviated. Genus *Discotarbus* Petrunkevitch.
 — Carapace with rounded posterior corners and an elongated elevation in place of an eye-tubercle. Only four anterior tergites abbreviated. Genus *Metatarbus* Petrunkevitch.

Genus *Architarbus* Scudder, 1868Type *A. rotundatus* Scudder

Carapace much longer than wide, rhomboidal, posteriorly produced far beyond the level of its lateral corners. Posterior edge concave on sides, strongly convex in middle. Sides of carapace convex, converging, then concave beyond the eyes and ending in a sharp point. The carapace is high, with sloping sides and a pair of sessile eyes in front, about one quarter of the total length of the carapace from the anterior point. Six anterior tergites abbreviated and procurved in a progressively lesser degree from the first to the sixth. Either the first tergite alone or both the first and second may be overlapped in middle by the end of the carapace, producing the impression that they are composed of a pair of sclerites. The median line dividing the abbreviated tergites present, but not always visible. First pedal coxae contiguous along their entire inner edge, concealing from view the pedipalpal coxae. Number of sternites eight.

Two American species belong to this genus. They may be distinguished as follows:

- a. Posterior end of carapace reaches with its middle point the posterior end of the *third* sternite (when superimposed on photographs made at the same magnification). Sixth tergite not much shorter in middle than at the sides. *A. rotundatus*.
- b. Posterior end of carapace reaches beyond posterior end of *fourth* sternite. Sixth tergite much shorter in middle than at sides. *A. minor* (Figure 12).

Architarbus rotundatus Scudder, Geol. Survey Illinois, 1868, Vol. III, p. 568. Petrunkevitch, Trans. Conn. Acad., 1913, p. 125, Plate VII, figs. 74-79, Text-figures 79-80. Scientific Papers, State of Illinois, 1945, Vol. III, No. 2, p. 20, fig. 1.

This is a common species. To the seventeen specimens listed by me in 1913, the specimen in the Illinois State Museum must now be added. They are all from the Pennsylvanian of Mazon Creek, Illinois. The type is in the collection of the University of Illinois.

Architarbus minor Petrunkevitch, Trans. Conn. Acad., 1913, Vol. 18, p. 128. Plate XIII, figs. 81, 82. Text-figures 81-82.

Scientific Papers, State of Illinois, 1945, Vol. III, No. 2, p. 21, Text-figure 2.

A single specimen, No. 189, in the collection of Peabody Museum, Yale University, from the Pennsylvanian of Mazon Creek, Illinois.

Genus *Hadrachne* Melander, 1903

Type *H. horribilis* Melander

Carapace slightly longer than wide, acutely pointed in front, without eyes. Posterior edge gently procurved. Abdomen ovoid. Six tergites abbreviated.

Hadrachne horribilis Melander, Jour. Geol., 1903, Vol. XI, p. 180, Plate V, fig. 1, Plate VIII, fig. 1.

Petrunkevitch, Trans. Conn. Acad., 1913, Vol. 18, p. 130, Plate XII, fig. 71, Text-figures 83, 84 (sub *Architarbus*).

Id. Scientific Papers, State of Illinois, 1945, Vol. III, No. 2, p. 22.

A single specimen, type, No. 9232, in the Walker Museum of the University of Chicago, from the Pennsylvanian of Mazon Creek, Illinois.

Genus *Leptotarbus* Petrunkevitch, 1945

Type *L. torpedo* Pocock, sub *Geraphrynus*

Carapace much longer than wide, acutely pointed in front, without eyes. Posterior edge evenly rounded, procurved. Sides almost straight in posterior two thirds, rapidly converging anteriorly. Abdomen nearly twice as long as wide. Five tergites abbreviated.

Leptotarbus torpedo (Pocock), Terrestrial Carboniferous Arachnida, 1911, p. 54, Plate III, fig. 1, Text-figures 26, 27 (sub *Geraphrynus*).

Petrunkevitch, Scientific Papers, State of Illinois, 1945, Vol. III, No. 2, p. 23.

A single specimen from Coseley, near Dudley, No. 10 of the collection of Walter Eggington.

Genus *Mesotarbus*, newType *M. intermedius* n. sp.

This genus differs from *Goniotarbus*, to which it is related, by the proportions of its carapace and the shape of the posterior edge of it. The carapace is considerably longer than wide, strongly pointed in front and its posterior edge is so strongly procurved that the creature could be mistaken for a species of *Architarbus* were it not for the fact that the latter has only one pair of eyes which are sessile, whereas *Mesotarbus* has a trifoliate eye-tubercle with three pairs of eyes. The strong curvature of the posterior edge of the carapace is the cause of the sigmoid shape of the three anterior tergites resembling the condition found in *Architarbus*.

Mesotarbus intermedius n. sp. (Figures 134, 135 and 242)

Type. Specimen In. 18506. A single piece from the Upper Coal Measures of Coseley, Staffs, presented by S. Priest to the British Museum in January 1917. It shows only the dorsal surface. The tip of the abdomen is broken off. Nevertheless, this remarkable little specimen is of special interest because of its characters which are intermediate between those of *Architarbus* and *Orthotarbus*. Of course, this does not mean that it may be regarded as the ancestral type of *Architarbus*. It is more likely that the same evolutionary trend manifested itself in species with a trifoliate eye-tubercle as in those with a pair of sessile eyes, namely the trend to increase the size of the carapace by its backward growth considerably beyond its original line of juncture with the abdomen. In other words, *Mesotarbus* in my opinion is not a link between *Orthotarbus* and *Architarbus*, but an example of an evolutionary trend reaching its apex in *Mesotarbus* in the one series and in *Architarbus* in the other series.

Total length ca. 10 mm. Carapace 4.72 mm. long, 3.86 mm. wide. First leg, femur 1.0, patella 1.0, tibia 1.1, metatarsus 0.8, tarsus 0.9. Total length of first leg 4.8 mm. Second leg, femur 1.1, patella 1.4, tibia 1.5, rest of leg missing. Third leg, femur 1.7, rest missing. Fourth leg, femur 1.7, rest missing. If one can judge by the relative length of the femora alone, the fourth and third legs must have been considerably longer than the first and second.

The carapace is very flat and smooth. Its anterior point is drawn out as a thorn-like projection. In consequence of this the lateral edges of the carapace are concave in their anterior quarter. The

posterior edge is evenly rounded, strongly procurved as shown in the drawing. The eye-tubercle is very low, yet quite distinct. The eyes are clearly visible. The first pair is separated by about two diameters, the third pair by twice that distance. The surface of the carapace shows the outlines of the coxae on the left side, and of the first, triangular abdominal sternite. They are shown by dotted lines in the figure. Six abdominal tergites are abbreviated, but only the first five are longitudinally divided by a median line and have, each, a pair of tiny tubercles. These five segments are also longer at their sides than in their middle and each half of the anterior three tergites is sigmoid in shape. The sixth and the following tergites are straight.

Specimen No. 18344 of the S. Priest collection from the same location belongs to this species. It is represented by a single piece showing only the ventral surface, but with the outline of the carapace superimpressed. The ends of the palpi are visible. Part of the abdomen is missing. Total length 11.3 mm. Carapace 5.14 mm. long, 3.86 mm. wide.

Genus *Goniotarbus*, new

Type *G. tuberculatus* n. sp.

This genus differs from *Mesotarbus* by the shape of its carapace which is wider than long, and from *Mesotarbus* and *Orthotarbus* by the angular shape of the posterior edge of the carapace, which is procurved in *Mesotarbus* and straight in *Orthotarbus*. The genus is represented by six specimens, all from the same locality, Upper Carboniferous Coal Measures of Coseley, Staffs., in the collection of the British Museum and all belonging to the same species.

Goniotarbus tuberculatus n. sp.

Figures 130-133 and 238-241

Type, In. 31249. Two pieces, collected by W. Egginton, November, 1932.

Paratype. In. 15864. Two pieces. Purch. J. R. Gregory, Jan. 1911.

Paratype. In. 22840. Two pieces. Wheelton Hind collection, 1921.

Specimen In. 18339. Two pieces, Presented by S. Priest, April, 1916.

Specimen In. 18340. Single piece, S. Priest collection.

Specimen In. 31252. Two pieces, No. 24 of the W. Egginton collection.

Description of Type. In. 31249. Figures 130-132, 340-341.

Total length 22 mm. Carapace 7.0 mm. long, 8.5 mm. wide. First leg, femur 2.86, patella 2.29. Second leg, femur 2.86, patella 2.29. Third leg, femur 3.57, patella 3.00. Fourth leg, femur 4.29, patella 3.29, tibia 3.29, metatarsus 1.86, tarsus 1.00, total 13.73. Probable order of legs 4312.

Except for the tip of the abdomen the dorsal surface of the body is well preserved, although the granulation of the matrix of the nodule makes the study of such structures as the eyes rather difficult. The impressions of the coxae are visible on the surface of the carapace. The sides of the carapace are nevertheless plainly visible; they are convex and converge to a point in front of the eye-tubercle. The posterior edge of the carapace is also plainly visible; it is transversely straight in its middle third and forms distinct angles which are somewhat raised and project above the first tergite. The eye-tubercle shown under somewhat greater magnification in Figure 132 has rather steep sides so that the eyes are situated at a considerable angle to the plane of the carapace. Only four eyes can be made out, and then only by examining the tubercle in different positions and changing the angle of the incident ray of light. The abdominal tergites are plainly visible. The anterior six are abbreviated, divided by a median line and provided each with a pair of distinct tubercles which appear in the specimen as deep, somewhat transversely elongated pits. The pair of longitudinal lateral lines of the ventral surface are superimpressed over the dorsal surface, but are omitted from the drawings (Figures 130 and 240).

The piece showing the ventral surface of the specimen (Figures 131 and 241) is in some respects better preserved than the dorsal one, but in other respects is more confusing inasmuch as the abdominal tergites appear even more deeply impressed than the sternites. Only comparison with other specimens permits the disentangling of the structures actually belonging to the one or the other surface. It seems certain however, that the seventh, eighth and ninth tergites coincide with the corresponding visible sternites and therefore belong to the same abdominal segments. The sternum is well visible, but its structure is not clear. The coxae show well, as figured in the drawing. The minute coxae of the pedipalpi, visible between the coxae of the first pair of legs, show two spinelike projections. The palpi are very slender and short. Only the distal three joints are visible. The legs are much more slender than in the American representatives of the genus.

Paratype In. 15864 (Figure 238). Total length ca. 19 mm. Carapace 6.86 mm. long, 7.86 mm. wide. None of the legs preserved. The piece representing the mold of the dorsal surface shows the structure of the carapace clearly. The eye-tubercle is typical of the genus, with steep sides. The pair of anterior eyes are preserved best. They appear as flat discs with a diameter of 0.30 mm., and can be measured very accurately on account of the sharpness of their circumference. The left posterior eye is also well preserved and has approximately the same diameter. The other three eyes are not distinct. The surface of the carapace is distinctly punctured, i.e., it was granular in life. The abdomen is smooth. All ten tergites are clearly visible with paired tubercles on the anterior six abbreviated tergites. The intersegmental line between the ninth and tenth tergites is rather faint. Outlines of sternites and of the anal operculum are superimpressed over the tergites, but their number cannot be ascertained. The second piece of this specimen is a natural cast of the first. The carapace shows the two posterior lobes particularly well, raised above the surface of the abdomen, and projecting behind the anterior edge of the first tergite. Between the lobes there is a central depression. The entire surface of the carapace is granular. Impressions of coxae are visible, but the anterior edge is missing and the eye-tubercle does not show. The abdomen is complete and the sternites show more clearly than on the piece representing the mold, but their number cannot be ascertained because the tergites are also present and interfere with the interpretation of the anterior region. The anal operculum is clearly visible.

Paratype In. 22840. (Figures 133 and 239). Total length 21 mm. Carapace 6.86 mm. long, 7.14 mm. wide. None of the legs preserved. Piece *a* shows the complete dorsal surface of the body. The surface of the carapace is evenly punctured, the eye-tubercle even more coarsely punctured than the rest. The first and second pair of eyes are well preserved. Three of the eyes appear as strongly convex bodies, the left second eye only as a flat disc. The difference in shape is undoubtedly due to a difference in preservation of the corneal lens. The third pair is not preserved. The posterior lobes of the carapace are well developed. The tergites are clearly visible, but the intersegmental line between the ninth and the tenth tergites is very faint. The abbreviated tergites show the paired tubercles in their normal position and number. The anal operculum appears only as

a faint depression. Between the paired tubercles the tergites show that their surface is deeply punctured. On one side of the carapace all four trochanters are visible. On the other side of the specimen the impression of a fossil plant is present.

Piece *b* shows the entire ventral surface of the body and is particularly valuable for its remarkably clear and perfect preservation of all structures. The small pedipalpal coxae appear wedged in between the slightly diverging anterior ends of the first pedal coxae which are contiguous with each other in their posterior half. All coxae are more or less triangular in shape and those of the second and third pair are separated by the sternum, while those of the fourth pair meet by their apices just behind the sternum. The structure of the sternum itself is also very well visible. It consists of an anterior hexagonal sclerite with parallel sides, a pair of median pentagonal sclerites which are in contact with each other along the median line, and a posterior hexagonal sclerite so arranged that the sternum appears to be truncated behind. The abdomen is also very well preserved. It is almost free from superimpressed dorsal intersegmental lines. The first sternite is triangular and occupies the entire space between the fourth coxae. The second sternite is unusually short and shows a pair of faint, circular impressions of seminal receptacles. The third sternite is recognizable as such by the diverging longitudinal lines which run parallel to each other in the following segments and divide the sternites into three fields, typical for all Architarbi. In the middle portion of the third sternite a trapezoidal area is outlined by distinctly raised lines. I interpret this area as the ventral, evertible, respiratory sac, comparable to those figured by me in American Architarbi. The fourth sternite is somewhat shorter than the third. The fifth is about as long as the third. The line between the last sternites, and the anal operculum are very faint. The lateral soft pleura is plainly visible.

Specimen In. 18339. This specimen is distinctly smaller, being only about 14.5 mm. long, with a carapace 5.4 mm. long, 6.0 mm. wide. Both pieces show only the dorsal surface and that not perfectly. Three impressions of coxae appear on one of the two pieces as fairly deep molds, on the other as natural casts obstructing the view of the eye-tubercle. On this same piece the abdomen is incomplete, but on the other piece all tergites are visible. The presence of posterior raised lobes on the carapace, its proportions and the

paired tubercles on the abbreviated abdominal tergites are so characteristic that the small size of this specimen may be safely explained as a youthful character.

Specimen In. 18340, is a poorly preserved single piece showing only the ventral surface. Portions of the carapace and its outline are superimpressed over the coxae, making the study of both the coxae and the carapace unsatisfactory. Although the posterior end of the abdomen is broken off, the segmentation and appearance of the anterior three quarters fully agree with those of the type. Total length 17.7 mm. Carapace 6.43 mm. long, 7.71 mm. wide.

Specimen In. 31252, is probably a young individual of this species. At least the presence of some tubercles on the abbreviated tergites speaks in favor of this assumption. The other characters are too poorly preserved and the carapace shows only a tiny piece. Only the abdomen is complete.

Genus *Orthotarbus* Petrunkevitch, 1945

Type *O. minutus* Petrunkevitch

Carapace wider than long, pointed in front, with a straight posterior edge. Sides concave in front of the eye-tubercle, convex posterior to it. Trifoliate eye-tubercle with three pairs of eyes. Pedipalpal coxae partly visible. Palpi slender and small. Five or six tergites abbreviated. Two American species which can be distinguished as follows:

- a. Size smaller, maximum length 10.6 mm. Ratio of length to width of carapace 3 : 3.5 *O. minutus*.
- b. Size larger, 16.5 to 19.0 mm. Ratio of carapace 3 : 4. *O. robustus*.

Orthotarbus minutus (Petrunkevitch) sub *Geratarbus*, Trans. Conn. Acad., 1913, Vol. 18, p. 119, Plate XI, fig. 69, Text-figures 73-74. Id., Scientific Papers, State of Illinois, 1945, Volume III, No. 2, p. 28, Text-figures 7 and 8.

Seven specimens from the Pennsylvanian of Mazon Creek, Illinois, all in the collection of Peabody Museum, Yale University.

Orthotarbus robustus Petrunkevitch, Scientific Papers, State of Illinois, 1945, Vol. III, No. 2, pp. 29-36, Plate III, figs. 14-16, Plate IV, figs. 18-21 and 23. Text-figures 9-14.

Five specimens from the Pennsylvanian of Mazon Creek, Illinois, all in the collection of the Illinois State Museum, Springfield, Ill.

Genus *Ootarbus* Petrunkevitch, 1945

Type *O. pulcher* Petrunkevitch

Carapace wider than long, evenly rounded in front, with an almost straight or slightly sinuous posterior edge. Trifoliate eye-tubercle with three pairs of eyes present. Pedipalpal coxae partly visible. Five tergites abbreviated.

This genus is represented by two American species which may be separated as follows:

- a. Posterior edge of carapace almost straight, evenly and slightly procurved. *O. pulcher*.
- b. Posterior edge slightly sinuous, procurved in middle, recurved on sides. *O. ovatus*.

Ootarbus pulcher Petrunkevitch, Scientific Papers, State of Illinois, 1945, Vol. III, No. 2, pp. 36-41, Plate III, figs. 12, 13, 17, 22. Text-figures 15-22.

Three specimens from the Pennsylvanian of Mazon Creek, Illinois, in the collection of the Illinois State Museum, Springfield, Ill.

Ootarbus ovatus Petrunkevitch, Scientific Papers, State of Illinois, 1945, Vol. III, pp. 41-42. Plate I, figs. 5, 6. Text-figures 23.

A single specimen from the Pennsylvanian of Mazon Creek, Illinois, in the collection of the Illinois State Museum, Springfield, Ill.

Genus *Phalangiotarbus* Haase, 1890

Type *P. subovalis* (Woodward), sub *Architarbus*

Phalangiotarbus subovalis (Woodward), sub *Architarbus*, Geol. Mag. 1872, Vol. IX, p. 385, Plate IX, figs. 1 a-b.

Haughton, S., Journal Royal Geol. Soc. Ireland, 1877, Vol. XIV, pp. 222-223, figs. 1 and 2.

Petrunkevitch, 1948 (Amer. Jour. Sci., Vol. 246, pp. 353-362, Text-figures 1-4; Plate 1.

Three specimens from the Middle Coal Measures of Burnley, Lancashire. Specimen F 103 is in the Trinity College Museum, Dublin. The location of the other two specimens, including the type, is not known to me.

Genus *Geratarbus* Scudder, 1890

Type *G. lacoei* Scudder

Carapace wider than long, rectangular, with almost straight posterior edge and with a straight anterior edge with a small triangular

projection in front of the trifoliate eye-tubercle bearing three pairs of eyes. Pedipalpal coxae partly visible. Five tergites abbreviated.

This genus is represented by a single species, the genotype.

Geratarbus lacoiei Scudder, Mem. Boston Soc. Nat. Hist., 1890, Vol. IV, p. 448, Plate 40, fig. 11.

Petrunkevitch, Trans. Conn. Acad., 1913, Vol. 18, p. 118, Plate XI, fig. 68, Text-figures 71, 72.

Already in 1913 I expressed the opinion that the "more or less triangular depression with rounded angles and emarginate sides," situated immediately behind the anterior projection of the carapace is "probably the eye tubercle." Thirty years later I discovered the three pairs of eyes on the trifoliate tubercle in several species of American Palaeozoic Architarbi and figured them in 1945. But on account of war conditions I was not able at that time to reexamine the type of *G. lacoiei*. Now, owing to the courtesy of Dr. A. Wetmore, Director of the U. S. National Museum, and Dr. R. S. Bassler, Curator, to both of whom I am deeply indebted for the privilege accorded me to study the specimen in our laboratory here, I am able to add to my old description the following new observations. 1) The anterior edge of the carapace has a small, triangular projection in front of the eye-tubercle (not truncated as was shown by me in 1913 in figure 71, but pointed). 2) The five abbreviated tergites are bisected by a fine median line as in other Architarbi. 3) The transverse line shown in my former figure 72 is the intersegmental line between the second and third sternites. No sternites could be exposed by cleaning posterior to this transverse line because that part of the abdomen shows only the tergites. 4) In front of the intersegmental line a transversely elongated genital opening is now visible. 5) In front of the genital opening the small, triangular, first sternite is now clearly outlined by the intersegmental line separating it from the second sternite bearing the genital opening. 6) All three pairs of small eyes are visible on the trifoliate tubercle. Their arrangement is of the same type as in *Orthotarbus* and *Ootarbus*.

The rest of the old description is correct.

The type and only specimen from the Pennsylvanian of Mazon Creek, Illinois, is in the U. S. National Museum, (No. 37966).

Genus *Metatarbus* Petrunkevitch, 1913

Type *M. triangularis* Petrunkevitch

Carapace wider than long, triangular, with sides and posterior

edge convex. Angles rounded, anterior end bluntly pointed. Eyes wanting, but an elongated elevation present in place of an eye-tubercle. Pedipalpal coxae partly visible. Four tergites abbreviated, anterior three procurved, the fourth with recurved posterior edge.

This genus is represented by a single species, the genotype.

Metatarbus triangularis Petrunkevitch, Trans. Conn. Acad., 1913, Vol. 18, pp. 122-123, Plate XI, figs. 66, 67, Text-figures 77, 78.

Id., Scientific Papers, State of Illinois, 1945, Vol. III, No. 2, p. 24, Text-figures 3 and 4.

Two specimens, both from the Pennsylvanian of Mazon Creek, Illinois. The type, No. 182, in the Peabody Museum, Yale University. The other specimen in the Museum of Comparative Zoology, Harvard University.

Genus *Discotarbus* Petrunkevitch, 1913

Type *D. deplanatus* Petrunkevitch

Carapace slightly wider than long, flat, triangular, with sides and posterior edge convex, without eyes or eye-tubercle. Abdomen flat, disc-shaped. Six tergites abbreviated, anterior three procurved, the following three straight. Pedipalpal coxae visible, reaching the sternum.

This genus is represented by a single species, the genotype.

Discotarbus deplanatus Petrunkevitch

Trans. Conn. Acad., 1913, Vol. 18, p. 120-121, Plate XII, fig. 10, Text-figures 75, 76.

Id., Scientific Papers, State of Illinois, 1945, Vol. III, No. 2, p. 23, Plate I, fig. 7.

Three specimens from the Pennsylvanian of Mazon Creek, Illinois. The type, No. 174, and Specimen No. 175 in the collection of Peabody Museum, Yale University. Specimen No. 14869 in the Illinois State Museum.

Genus *Paratarbus* Petrunkevitch, 1945

Type *P. carbonarius* Petrunkevitch

Carapace triangular, wider than long, with sides and posterior edge convex, anteriorly pointed. A pair of sessile eyes on a very low ellipsoidal elevation. Pedipalpal coxae visible. Six tergites abbreviated.

This genus is represented by a single species, the genotype.

Paratarbus carbonarius Petrunkevitch

Scientific Papers, State of Illinois, 1945, Vol. III, No. 2, pp. 25-27, Plate II, fig. 11, Text-figures 5 and 6.

A single specimen from the Pennsylvanian of Mazon Creek, Illinois, in the Illinois State Museum.

Key to the European Species of Architarbi

1. Carapace evenly rounded in front, with a straight posterior edge. *Phalangiatarbus subovalis* Woodward.
— Carapace pointed in front 2
2. Carapace longer than wide 3
— Carapace wider than long or as wide as long 5
3. Carapace with a trifoliate eye-tubercle bearing three pairs of eyes. Abbreviated tergites each with a pair of tubercles situated close together. *Mesotarbus intermedius* n. sp.
— Carapace without tubercle or eyes 4
4. Width of body one third of total length. Anterior two tergites sinuous. *Leptotarbus torpedo* (Pocock) sub *Geraphrynus*.
— Width much more than one third of total length. Anterior four tergites sinuous. Pocock's species *angustus* (sub *Geraphrynus*).
5. Carapace with a trifoliate eye-tubercle bearing three pairs of eyes. Abbreviated tergites each with a pair of tubercles situated close together. Posterior edge of carapace angulate. *Gomotarbus tuberculatus* n. sp.
— Carapace either without eyes or (*secundum* Pocock) with only one pair of eyes 6
6. Posterior edge of carapace sinuous 7
— Posterior edge either angulate, or procurved or straight 8
7. Last two intersegmental tergal lines form an angle directed with the apex forward. Pocock's species *angulatus* (sub *Geraphrynus*).
— Last two lines gently recurved. Pocock's species *hindi* (sub *Geraphrynus*).
8. Posterior edge of carapace straight. Two last tergal intersegmental lines form an angle directed with its apex for-

- ward. Waterlot's species *kliveri* (sub *Opiliotarbus*).
- Posterior edge procurved. None of the tergal lines angulate in middle 9
9. Posterior edge of carapace angulate. Abbreviated tergites each with a pair of tubercles situated close together. A single pair of eyes, according to Pocock. Pocock's species *tuberculatus* (sub *Geraphrynus*).
- Posterior edge of carapace not angulate, but evenly curved. Abbreviated tergites without tubercles. A single pair of eyes, according to Pocock. Pocock's species *eggintoni* (sub *Geraphrynus*).
-

NB. The Genus *Eotarbus* Kusta is not included in the above key for the following reasons. Kusta (73) listed on p. 7 of his article in 1885 under No. 14 a specimen under the Genus *Architarbus* with a question-mark. In 1888 he named it *Eotarbus litoralis* and gave a figure of it. He gave no description of the specimen which, according to Fritsch (23) has apparently been lost. Haase regarded it as an architarbid, but Fritsch believed it to be an insect larva. The figure resembles an *Opiliotarbus*, but without a description of the specimen and in view of its loss nothing can be done about it.

2. Family OPILIOTARBIDAE, 1945

The characters of this family are given in the key. A single genus belongs to it.

Genus *Opiliotarbus* Pocock, 1900

Type *O. elongatus* (Scudder), sub *Architarbus*

Pedipalpal coxae not visible. First pedal coxae in contact with each other in the median line along their full length. Carapace evenly rounded in front, with a straight posterior edge, wider than long. Eyes wanting. A single species.

Opiliotarbus elongatus (Scudder), sub *Architarbus*, Mem. Boston Soc. Nat. Hist., 1890, Vol. IV, p. 449, Plate 40, fig. 4.

Pocock, Geol. Mag., 1910, Vol. VII, p. 511.

Petrunkévitch, 1913, Trans. Conn. Acad., Vol. 18, p. 131, Plate XI, figs. 62-65. Text-figures 85-88.

Two specimens from the Pennsylvanian of Illinois: the type, No. 37975, from Mazon Creek; specimen No. 37970 from Braidwood; both in the U. S. National Museum.

The specimen from Belgium, referred to this genus by Waterlot in 1934 under the name of *O. kliveri* does not belong to it. Its trochanters are not known, its carapace is triangular, the number of its tergites is given as nine. These are characters found only in the Family Architarbidae, q.v.

3. Family HETEROTARBIDAE Petrunkevitch, 1913

This is an aberrant family with some characters resembling Opliones and others Architarbi. It is represented by a single specimen.

Genus *Heterotarbus* Petrunkevitch, 1913

Type *H. ovatus* Petrunkevitch

Heterotarbus ovatus Petrunkevitch, Trans. Conn. Acad., 1913, Vol. 18, p. 115, Plate X, fig. 59, Text-figure 70.

The specimen is from the Pennsylvanian (Lower Allegheny) of Mazon Creek, Illinois, and is in Mr. L. E. Daniels' collection. No other specimen has as yet been found.

5. Order ACARI

The great majority of Recent Acari are minute animals. A single Paleozoic species, *Protacarus crani*, has been described so far by Hirst from the Devonian Rhynie Chert Bed of Aberdeenshire. Hirst gave several excellent figures leaving no doubt of the affiliation of these fossils. The size of his specimens varied from 290 to 440 micromillimeters. It seems strange that the much larger representatives of the Family *Ixodidae* having always a very tough skin which resists mechanical injury, have not yet been found in the Paleozoic. Recent *Ixodidae* are visiting parasites of Vertebrates, mainly of Mammals and Reptiles. Recent Acari are either parasitic, terrestrial or inhabitants of fresh- and sea-water.

Modern Acarologists are inclined to split the Order Acari into several Orders. Oudemans has even attempted to split the single Order Acari into several groups to which he gave the rank of Classes. His classification is based on the movability or immobility of the coxae, a character which exhibits remarkable fluctuations in other orders of Arachnida. When, as in scorpions, in the same individual

the first two pairs of coxae are movable and the third and fourth pairs are permanently fused on each side of the body, the use of the state of mobility as an important character is quite unwarranted. The raising of Suborders to the rank of Orders is quite another matter, for they are well defined in their characters. Yet I think that they show sufficient characters in common with each other to necessitate their retention in a single Order Acari. The Order shows a tremendous amount of variation in structure and habits, presumably correlated with parasitism. The interested reader is referred to Count Herman Vitzthum's ACARI in Kükenthal's Handbuch der Zoologie, 1931. Volume 3, second half, pages 1-160 with an extensive bibliography.

II SUBCLASS STETHOSTOMATA, new

In this Subclass are united the only two Orders of Arachnida in which the arrangement of the coxae is similar to that in Xiphosura and Eurypterida and, therefore, unlike that in all other orders of Arachnida. Morphologically anterior to the pedipalpal coxae, the chelicerae are in reality situated *above* them in all Arachnida except the Stethostomata. In the latter all six pairs are in the same plane and, in addition, the coxae of the three-jointed chelicerae are so wedged in between the coxae of the pedipalpi that the mouth, to be functional, had to move backwards until it became situated between the coxae of the first pair of legs, behind the posterior ends of the cheliceral and pedipalpal coxae. The abdomen is broadly joined to the cephalothorax and its first segment is complete with a tergite and a sternite, though the former is usually concealed under the carapace and becomes exposed only occasionally, when the abdomen and the cephalothorax are disrupted or at least fully stretched. The number of abdominal segments is fixed, ten in one of the Orders, eleven in the other. Anus with an operculum. Respiration by means of two or three pairs of book-lungs, dependent upon the Order. The separation of the Orders is simple, as indicated in the key. Both Orders are extinct, found only in the Palaeozoic.

6. Order HAPTODA

Introductory Remarks.

This Order of fossil Arachnida was established by Pocock in 1911, when he proposed it for the inclusion of a single species, *Plesiosiro madeleyi*, found in the Upper Carboniferous Coal Measures at Coseley,

near Dudley, England, in a bed of nodular ironstone about ten feet above the "ten yard" coal. It was established primarily on the basis of segmentation of the first tarsi, for Pocock was not acquainted with the other characters peculiar to this Order. From his statements it is not quite clear how many specimens he had at his disposal. There must have been at least five, because Pocock mentions besides the type in the "collection of the late Mr. William Madeley," "other specimens in Mr. Madeley's, Dr. Hind's, Mr. Priest's, and Mr. Egginton's Collections." (p. 44.) None of these specimens was complete. The type, according to Pocock, "shows the basal segments of the mandibles, the two palpi, one complete leg of the first pair, the femur, patella, and half the tibia of the third leg, the femur and patella of the fourth, and the femur of the second; the shape of the carapace and the tergal plates of the opisthosoma. Also the posterior sterna of the opisthosoma; and the hollow spaces of the basal segments of the legs of the first pair." (p. 44.) The other specimens studied by Pocock "show additional features which made it possible to restore the dorsal surface tolerably completely. Details of the ventral surface are in no instance well preserved." (p. 44.) Thus Pocock's description of the characters of the species was, of necessity, based on a comparative study of several specimens, on the assumption that they belonged all to the same species. That such an assumption is not always safe, is demonstrated by the fact that of his four paratypes the one of the Wheelton Hind Collection now belonging to the British Museum and sent to me for study, after having been subjected to careful cleaning proved to be not a *Plesiosiro* at all, but a member of the quite remote Order Phrynichida, presumably a *Graeophonus anglicus* (q.v.). However, the other three paratypes undoubtedly belong to the same species as the type. Unfortunately, the specimens were not sufficiently cleaned and the structures were not adequately exposed to view at the time when Pocock studied them. This circumstance was responsible for the fact that some of his statements are not correct. Still it remains to his eternal credit that he sensed the existence of a distinct type of an Arachnid and created for it a new Order. The strict rules of the British Museum made it impossible for me to examine and study the type. But I have had the privilege of handling all of Pocock's paratypes. After cleaning them of the white mineral obstructing the view of the true surface of the specimens, the tarsus of the first leg in the paratype In. 22835 and the tarsi of the third and fourth legs in the paratype

In. 18341 became exposed to view through the removal of the matrix with the aid of an engraver's chisel. Thus I was able to study structures which remained invisible before. In addition to Pocock's paratypes, the collection of the British Museum, which was sent to me, contained three other specimens which I treated in a similar manner. Of these specimens, the one numbered In. 7922 is almost complete and exceedingly well preserved, while the other two, although not as perfect as the first, are yet more complete and better preserved than Pocock's paratypes. Thus the characters of the Order, as given here, differ in several essential respects from those given by Pocock. They are based on a study of six specimens, three of which are Pocock's own paratypes. The disposition of the coxae became fully understandable only after their comparison with a similar disposition in *Anthracomarti* and after prolonged study of the sterno-coxal region in all Orders of Arachnida and in Eurypterida and Xiphosura. There is no doubt in my mind that the characters of the type, if the latter were to be properly cleaned and the concealed features exposed to view, would fully conform with the characters given here.

Characters of the Order. Terrestrial fossil Arachnida with broad juncture between the cephalothorax and the abdomen. Carapace entire, with a single pair of eyes situated close together near its anterior end. Abdomen composed of eleven segments, not counting the anal operculum. Each abdominal segment with a tergite and a sternite, laterally connected by a distinct, soft, not segmented pleura, lacking only in the first and the eleventh segments. First sternite triangular, bordered on its sides by the posterior edges of the coxae of the fourth pair of legs. The second, genital sternite very large, extending posteriorly to the end of the second fifth of the total length of the ventral surface of the abdomen. The third to tenth sternites are much shorter and are longitudinally divided by a fine, median line. The eleventh sternite encloses the transversely elliptic anal operculum. The first tergite is very short, partly or almost entirely concealed by the posterior end of the carapace which is as wide as the abdomen. The second tergite is of normal length and always exposed to view. The coxae of the pedipalpi are narrow and long, and are separated by the coxae of the chelicerae. The first pair of pedal coxae are wide apart, those of the fourth pair are contiguous by their proximal ends. Sternum narrow and long, composed of three sclerites. All coxae movable. Chelicerae three-jointed, chelate. Pedipalpi six-jointed, pedi-form; their first joint, the coxa, without maxillary process or lobe.

Legs seven-jointed. All trochanters single-jointed. Patella clearly distinct from the tibia. Tarsus of the first pair of legs six-jointed, those of the second, third and fourth pairs four-jointed. Respiration by means of two pairs of book-lungs situated in the second and third abdominal segments.

It may be properly questioned wherein does the above statement concerning the segmentation of the haptopod abdomen and asserting the existence of eleven segments differ from Pocock's interpretation of the abdomen. He says: "Opisthosoma longer than wide, narrowed posteriorly, rounded at the extremity, exhibiting in one case ten terga on the dorsal side, and always a small anal operculum beneath the last, but on the ventral side. Thus eleven segments are traceable in the opisthosoma." (p. 41-42.) The number eleven in both cases arises from the fact that Pocock included in his count the anal operculum as the eleventh segment, whereas I omit the operculum from my count because I consider it to be merely a differentiation of the last sternite and not the last tergite shifted ventrally and functioning as an operculum. Pocock's first tergite is my second tergite. The first tergite escaped Pocock's observation. In other words, the difference between our interpretation of the segmentation of the abdomen in Haptopoda is this: if we are to regard the anal operculum not as a differentiation of the last sternite, but as the last tergite, then we would have to admit the existence of twelve segments and not of eleven as Pocock does.

The correctness of my interpretation of the segmentation may be demonstrated in two different ways. If we superimpose photographs of the dorsal and ventral surfaces made at the same magnification, with outlines inked in and the rest removed by a reducer, we obtain a picture as the one shown in Figure 103. From this figure it will be seen that, beginning with the fourth sternite, all following sternites coincide with the tergites, proving that they belong to the same segments. The third sternite has both ends procurved, but its anterior ends coincide with the ends of the straight, third tergite. The second tergite falls within the limits of the second sternite, making it obvious that the first, abbreviated tergite belongs to the same segment with the triangular first sternite. This abbreviated first tergite is fully exposed in specimen In. 7922. In the paratype In. 18341 it is exposed on the observer's right side, but disappears under the carapace on the left side. Its posterior edge is somewhat thickened and overlaps the anterior edge of the following tergite, as usual in all Arthro-

poda. To show this more clearly, I made a cast, using a dental impression compound for this purpose. The result is shown in Figure 231 in which, photographically reproduced, the narrow first tergite is quite distinct. But suppose we were to deny its existence and interpret the narrow band behind the carapace as a connecting membrane between the carapace and the abdomen. Then we would be forced to admit that the first tergite disappeared completely and that the first sternite has no corresponding tergite. The number of segments would still be greater by one than the number given by Pocock. Theoretically such a disappearance could be expected, because it would conform with the evolutionary trend common to all Arachnida of the Subclass Latigastrea with which the Stethostomata share the type of abdominal juncture. Actually the structure in question has all the earmarks of a tergite and not of a membrane.

Pocock, in his description of the species on page 44, mentions the existence of "a narrow median granular crest on the anterior seven terga" and shows it in his Figure 15. The corresponding drawing of the ventral surface shows no such crest, nor is there any mention of a ventral crest in the text. Pocock was misled by what must have been a superimpression of lines. In the six specimens examined by me, the ventral surface of the abdomen exhibits a narrow, line-like crest extending from the middle of the third sternite to the anterior edge of the tenth sternite. This crest must have been in life a narrow groove, appearing as a ridge or crest on the inside of the abdominal wall. The dorsal surface shows an indefinite, shallow groove which is considerably wider than the ventral ridge and extends forward to the anterior end of the abdomen. In life it must have been a median groove on the inner surface of the abdominal wall. Whether it appeared as a crest on the outside of the body wall cannot be answered by considering only the evidence of the material available. At any rate, neither the ventral crest, nor the dorsal groove have the appearance of a structure separating the sclerites into a right and left one, though the ventral median crest looks more like the pair of ventral lines in *Architarbi* than the dorsal groove like the tergal lines in *Anthracomarti*.

Although, in his definition of the Genus *Plesiosiro*, Pocock speaks of the carapace as being "high," neither his own paratypes, nor the other specimens warrant this statement. It happens that the carapace is well preserved in all six specimens, and compared with such Arachnida as *Trigonotarbus* and *Cryptomartus* it produces the im-

pression of being rather low, resembling somewhat the carapace of scorpions. The abdomen is also rather flat, so that the transverse section through the body has the shape of an ellipse, the long axis of which (that is the one which corresponds to the transverse axis of the body), is from four to five times greater than the short axis which represents the dorso-ventral axis of the body. This shape, combined with the relative length of the legs makes the animal well adapted to terrestrial life. Owing to perfect preservation of all four legs in the same specimen, this feature of their anatomy stands now firmly established. The segmentation of all tarsi, not of the first pair alone as Pocock states, is a fact. The first tarsus of specimen In. 7922 and the third tarsus of specimen In. 18341 are shown photographically in Figures 233 and 234. Drawings of all four tarsi are shown in Figures 96 to 99. Since, however, the first tarsi have two more joints than the others, Pocock's assumption that the first tarsi had a tactile function comes as near truth as may be expected from a study of a comparatively rare fossil. At the same time it seems to me probable that the first tarsi, and possibly all the others as well, combined the function of tactile organs with that of chemoreception of an olfactory and perhaps even of a gustatory type, as in the case of many Insects. This assumption is the more probable because of the evidence derived by me from a study of the tarsi of Recent Ricinulei. Their tarsi are also segmented, somewhat as those of the Haptopoda, and show clearly numerous sense-organs which can be interpreted only as chemoreceptors. The existence of claws in Haptopoda could not be demonstrated, but if their claws were as difficult to see as are those of Recent Ricinulei, there is nothing surprising in their remaining invisible in fossil specimens.

The chelicerae, of which Pocock saw only the elongate, porrect basal segment, are fortunately well preserved in one specimen. As shown in Figure 100, they are chelate. Being in addition three-jointed, they add to the general similarity of the Haptopoda with Latigastra. But the position of the cheliceral coxae in the same ventral plane with the coxae of the other appendages and as far back as the coxae of the pedipalpi, between which they are situated, is very different from that in other Latigastra and, as stated above, much more like that in Xiphosura. The arrangement of the coxae is shown in Figure 25 and photographically in Figure 235. They are immediately recognizable by the four foramina, two for each coxa, a peculiarity existing also in *Anthracomarti* but in no other Arachnida. The anterior of these

foramina shows the evidence of articulation with the second joint. The posterior foramen seems to lead into a thorn-like process as in *Cryptomartus*, but I had no material at my disposal for ascertaining this point by longitudinal sectioning of the entire coxa. The chelicerae seem to be rather small and weak and could be used only for inflicting a small wound or holding small prey. In absence of powerful hands on the pedipalpi, such as scorpions and pseudoscorpions have for grasping and holding their prey, or lacking raptorial pedipalpi of the type found in Thelyphonida and Phrynichida, the Haptopoda must have been greatly restricted in the selection of their victims for food. Vegetal food is eliminated by the structure of their mouth parts. The Haptopoda must have either existed on minute creatures or else possessed powerful poison-glands. But the latter alternative finds no support in comparative anatomy. Perhaps the absence of poison-glands and the small size of their chelicerae made their existence gradually more and more precarious and was responsible for their early extinction.

The position of the genital opening, as tentatively indicated by Pocock in his Figure 16 and which he admits to be unknown, is contrary to our present knowledge of Arachnida and certainly wrong. While not apparent on the fossil specimens, it must have been located close to the posterior edge of the second sternite. It is possible that the sternite projects beyond the genital opening and thus hides it from view. Why the genital sternite of *Plesiosiro* is so large, remains of course unknown. That it is not a compound plate, produced by a fusion of two sternites, is quite certain, because all sternites are accounted for and because the existence of an additional segment would necessitate the assumption of a corresponding fusion of tergites, for which assumption there is no evidence, or else the disappearance of two tergites in front of the first visible one, which is also not supported by any evidence. The peculiar size and shape of the second sternite of *Plesiosiro* is, however, not unique in Arachnida. It resembles greatly the genital sternite of Thelyphonida. The latter are well known anatomically and embryologically because they survived from the Palaeozoic to the present time, the Order being well represented in hot and tropical countries. It is definitely known that the genital sternite of Thelyphonida is the sternite of the second embryonic abdominal somite. The entire ventral surface of the abdomen of *Plesiosiro* is shown photographically in Figure 232.

In five of the six specimens the lungs can be seen when the light

is properly arranged. Only paratype In. 18341 does not show them because its ventral surface is missing. The corrugations on the external covers of the lungs are visible in specimen 7922 on its left side and on one lung of the paratype In. 22837. The spiracles of these lungs are also visible. The lungs themselves are more or less triangular, the first spiracles are in direct continuation with the posterior edge of the genital sternite. The spiracles of the second pair of lungs appear as elongated slits at the posterior edge of the third sternite (figures 101 and 232).

The eyes undoubtedly belong to the type of simple ocelli. There is only one pair of them visible in each of the five specimens. In one specimen they have the appearance of flat, yellow discs, but in the other four, especially in specimen In. 7922 the complete lens is preserved. In this specimen the eyes are shown photographically in Figure 237. There is no eye-tubercle, but the position of the two eyes on the sides of what in life was a longitudinal ridge shows that their axis was directed outward, upward and slightly backward, so that the best vision must have been of objects situated to the left and right of the animal and somewhat above and behind it.

Family PLESIOSIRONIDAE Pocock

With the characters of the Order, as given above.

Genus *Plesiosiro* Pocock, 1911

Type *P. madeleyi* Pocock

New definition. Carapace relatively low, produced anteriorly into a short, pointed process. A median ridge separates a pair of round eyes, bifurcates a little behind them and continues as a pair of narrow crests which unite again not far from the posterior edge of the carapace. A pair of lateral crests, beginning as marginal tubercles, extend backwards almost to the posterior edge, at first slightly diverging, then again slightly converging. Lateral to these crests the sides of the carapace slope more or less steeply. The carapace is as long as wide. The anterior three pairs of coxae are separated by the sternum which is much longer than wide. The fourth coxae are contiguous by their proximal ends. Legs in order 1432. First tibia dorso-ventrally compressed, flat. Abdomen composed of eleven segments, not counting the anal operculum. First tergite abbreviated. First sternite triangular. Second sternite very large, as long as the four following together, with procurved (convex) posterior edge. Third

sternite with both edges procurved. Fourth to eight sternites with straight edges. Ninth and tenth tergites with recurved posterior edge (concave). Eleventh sternite enclosing the anal operculum biconvex. First tarsus six-jointed, the others four-jointed.

Plesiosiro madeleyi Pocock

Terrestrial Carboniferous Arachnida, 1911, p. 44.

The following description of the species is based on other specimens than the type.

Specimen In. 7922. Two pieces in the British Museum, from the bed of nodular ironstone, about ten feet above the "ten yard" coal, Coseley, Staffs. W. Madeley Coll. The specimen is shown photographically in Figures 229, 230, 232, 233, 236 and 237. Reconstruction of the species in Figures 94 and 95. Segmentation of the abdomen in Figure 103. Details of structure in Figures 96 to 102.

This remarkable specimen consists of two pieces of the same nodule, one showing the dorsal surface and hereafter to be referred to as piece *a*, the other showing the ventral surface and to be referred to as piece *b*. Piece *a* shows the carapace, the abdomen, the coxae of both chelicerae, three distal joints of both palpi, the complete first leg, pieces of the second leg, the femur of the third and fourth legs, portion of the coxa, trochanter and femur of the right first leg (the rest of it remaining hidden under the surface of the matrix), the second right leg complete except for the terminal tarsal segment, portion of the third right leg as far as the middle of its tibia, and portion of the fourth right leg as far as the end of its femur. Piece *b* shows the hand and fingers of both chelicerae (the left one less its movable finger), both palpi complete, portions of the first and second pairs of legs, portion of the left third leg as far as the middle of its femur, the right third leg complete, the coxa and femur of the fourth left leg and the complete fourth right leg; the sternum; eleven abdominal sternites; the two left lungs with their spiracles and the anal operculum.

Total length from the anterior tip of the carapace to the end of the abdomen—11.5 mm. Carapace 4.57 mm. long, 4.57 mm. wide at posterior edge which is straight. The sides are convex from the posterior angles to the outer edge of the second joint of the chelicerae (the only part of the chelicerae visible from above), hence concave to the anterior median point. The carapace is distinctly flat,

perhaps somewhat flatter than it was in life. Its median ridge is clearly outlined by two grooves running backward between the eyes, slightly diverging as far as the middle of the carapace, then just as slightly converging to a point a little before the posterior edge. The longitudinal line between the roof and the sloping side is clearly outlined on each side and begins with a distinct tubercle appearing as a pit in the specimen. The eyes are round, ca. 0.03 mm. in diameter and are separated from each other by their diameter. The surface of the carapace appears to be finely granular, but it is impossible to decide how much of this granulation may be attributed to the presence of fine punctures in life, rather than to the granular structure of the matrix itself.

The second joint of the chelicerae, visible only on piece *a*, is porrect, ca. 1.3 mm. long. The mesial edges of the pair appear as a single line, their outer edges are slightly, but distinctly converging. The second and third joint of the chelicerae are visible on piece *b*, between the two palpi. The hand is short and rather wide, the fingers slender, almost black, probably owing to carbonization, and both curved in the same direction, showing that in life they could have been brought in contact with each other along their entire length. The movable finger is mesial in relation to the immobile one, i.e. the two movable fingers are next to each other. The axis of flexion of the second joint is more or less transverse to the axis of the chelicera. Thus the motion of the hand was up and down and that of the movable finger—in and out. The latter direction leading to a closure of the fingers for taking hold of an object. The movable finger of the left chelicera is broken off and the immobile finger broken across its base and slightly dislodged to the left. The pedipalpi are definitely six-jointed, but their coxae are somewhat displaced and partly concealed under the fingers of the chelicerae so that they do not appear exactly as figured. They seem to be devoid of a maxillary process and in view of the position of the mouth *behind* them, such a process would be scarcely of any use. The limits of the sternum are not quite clear, but the outlines of the pedal coxae are quite distinct. Except for a slight displacement, they appear as shown in Figure 94. The coxae of the third pair of legs are cylindrical, but the others are more or less cone-shaped, the fourth pair being by far the longest. The legs are cylindrical, except the first tibia which is dorso-ventrally compressed and perfectly flat.

Legs	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	3.57	1.57	3.00	0.57	1.57	10.28
II	2.14	1.14	1.29	0.57	0.86	6.00
III	2.57	1.14	1.43	0.57	0.86	6.57
IV	3.57	1.57	2.00	1.00	1.14	9.28

Leg formula*	$\frac{1}{2.2}$	$\frac{4}{2.0}$	$\frac{3}{1.4}$	$\frac{2}{1.2}$
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* The leg formula was introduced by me for the first time in 1942, in my Study of Amber Spiders, p. 137. It is an expression of the relative length of the legs arrived at by simple division of their length by the length of the carapace.

The first leg is more slender than the others, and in contrast to them its tibia is quite flat and smooth. Its tarsus is composed of six segments and is more slender. The fourth tarsal joint of the second leg is missing, (it is present in specimen In. 18341). All four segments may be seen in the third tarsus which is reproduced photographically in Figure 234, while in the fourth tarsus the fourth segment is pressed out of its normal position as shown in Figure 99. A row of deep punctures is present on the fourth femur. Their regularity suggests that in life it may have been a row of elevated bases of sensory hairs, though it may have been simply a row of granules.

Except for its straight anterior edge by which it is attached to the carapace, the dorsal surface of the abdomen is neatly oval. Eleven tergites are present, the first of which is greatly abbreviated, the last—biconvex and quite small. A pair of granules is present on the second to fifth tergites (Figure 95). They may correspond to the attachment points of dorso-ventral muscles. The first sternite is triangular, with an apical angle of somewhat less than 90°. The second sternite is very large. Its anterior edge is practically straight, its sides parallel, its posterior edge strongly procurved (convex). The genital area is clearly indicated by a line-like groove, but no openings of receptacles are visible. The left lung-cover with its corrugations and the elongated spiracle are very distinct. The right spiracle is also well visible, but the right lung is indistinct and its view is partly obstructed by the right fourth leg. The third sternite is with both anterior and posterior edge procurved, but the posterior edge less so than the anterior one. This results in the third sternite being longer at its sides than in the middle where it is much shorter than the fourth sternite. The posterior edge of the latter is straight,

as is that of the following sternites. It is recurved (concave) in the ninth and tenth sternites. The eleventh sternite is small and bi-convex. A thin line divides the third to tenth sternites in two halves. The anal operculum is transversely elliptical. Its posterior border reaches the end of the abdomen.

Specimen In. 7923 is also of the W. Madeley Collection from the same horizon and locality as the preceding one. It is not nearly as well preserved nor as complete, yet is interesting in several ways. Its piece *a* shows the carapace with the eyes, the somewhat distorted tergites of the abdomen, the palpi and portions of five legs. Its piece *b* shows the same appendages including their coxae and the coxae of the chelicerae (Figure 235). Except for the fourth right coxa, all the other coxae and the sternum are very clearly outlined and the coxae of the first, second and third pairs of legs are of a color different from that of the matrix. They are partly superimposed one over another, and distinctly raised, leaving no doubt as to their movability. The right first and the left fourth legs are complete as far as the ends of their tibia. The four foramina of the chelicerai coxae are very conspicuous. The right lung is pressed in along its mesial edge, making it also very conspicuous. Total length of the specimen 11.43 mm. Carapace 4.72 mm. long. First femur 4.00 mm. long.

Specimen In. 15899 (No. 22 of the H. Johnson Collection purchased from J. F. Gregory, 25 Oct. 1913), is from the same horizon and locality as the preceding two. Piece *a* shows the carapace with the eyes, the abdominal tergites partly damaged, and the legs as far as the patella. Piece *b* shows the same portions of the legs, the sternum with the coxae, the first abdominal sternite and the entire dorsal surface of the abdomen as indicated by the straight intersegmental lines. The sternites, except the first just mentioned, are not visible. The interest and importance of this specimen lies in the excellent preservation of the sternum and its relation to the first pedal coxae. In front of the sternum the transversely elongated depression is evidently the mouth, but the area in front of the mouth is unfortunately entirely obliterated. Total length 10.29 mm. Carapace 4.29 mm. long. First femur 3.29 mm. Sternum in the shape of an elongated triangle, pointed behind, 1.60 mm. long, 0.90 mm. wide.

Specimen In. 22835, Pocock's paratype, originally of the Wheelton Hind collection, purchased in 1921, from the same horizon and locality

as the other specimens. Piece *a* shows the dorsal surface, piece *b*, the ventral. Both pieces were cleaned by me and on piece *b* the first right leg was exposed to the end of its tarsus by removal of the matrix. Only portions of other appendages are preserved on both pieces. The eyes are plainly visible. The abbreviated first tergite appears as a somewhat swollen ridge, but its nature is quite evident when one examines a well made cast. On the ventral surface, the sternum and the coxae are only faintly visible although the specimen is not in any way distorted. Clear impressions of tergites are superimposed over still clearer impressions of the sternites. The second sternite is of the same shape as in specimen 7922, but shows clearly *two round swellings* in the places shown on Figure 95. These swellings are probably sperm receptacles, and I think it safe to assume that the specimen is a mature female. Total length 10.57 mm. Carapace 4.29 mm. long. First leg, femur 3.15, patella 1.14, tibia 2.29, tarsus 1.00. Total length of first leg 7.89 mm.

Specimen In. 22837 is another of Pocock's paratypes from the same horizon and locality and originally in the same collection as the preceding specimen. Piece *a* shows only the dorsal surface, piece *b* shows the carapace with the eyes which are very faint, and the ventral surface of the abdomen. None of the appendages are preserved. The shape of the carapace makes its specific affiliation quite certain. Total length 11.57 mm. Carapace 4.43 mm. long.

Specimen In. 18341 is the third of Pocock's paratypes from the same horizon and locality. It was originally in Mr. S. Priest's collection and was presented by him to the British Museum in 1916. The specimen is incomplete inasmuch as it consists of a single piece presenting only the dorsal surface. After careful cleaning of the surface, features were exposed to view which were not mentioned by Pocock. The specimen now shows the carapace with its crests and eyes perfectly preserved; the first, abbreviated, and the second tergites, both complete, the following five tergites incomplete. The last four segments are missing. Both palpi are well preserved, each showing four segments. The first left leg, the third right and the fourth left legs are complete. Of the other legs only portions are preserved. The tarsal segmentation of the first and third leg is very clear, that of the fourth leg rather indistinct. The fourth right leg is so bent that it passes under the abdomen and becomes visible again beyond it. It is complete to the end of the first segment of its tarsus. The

carapace is 4.57 mm. long, 4.57 mm. wide, i.e. has the same dimensions as specimen No. 7922. The total length of specimen In. 18341 may be therefore estimated at probably 11.5 mm.

Legs	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	3.57	1.57	3.43	0.57	1.86	11.00
II	—	—	—	—	—	—
III	2.29	1.29	1.43	0.71	0.86	6.58
IV	3.57	1.29	1.86	1.29	1.00	9.01

Comparing these measurements with those of Specimen No. 7922 we notice at once their close similarity. The first leg is somewhat longer due to the slightly greater length of its tibia and tarsus. The fourth leg is slightly shorter, but the difference in both cases is not sufficient to be attributed to a difference in sex. I believe that all six specimens described here belong to the female sex and probably are all mature individuals.

A photograph of a cast of specimen 18341 is shown in Figure 231. It gives a clear idea of the appearance of the carapace as it was in life.

7. Order ANTHRACOMARTI, emended

Introductory Remarks.

The new facts concerning the arrangement of the coxae, the position of the mouth, the structure of the chelicerae and the segmentation and structure of the abdomen, brought to light in the course of the present investigation force me to restrict the Order Anthracomarti to species externally recognizable by the presence of five rows of dorsal plates in their abdomen. Consequently, the present definition of the Order and its classification differ considerably from that given in my Palaeozoic Arachnida of Illinois, published in 1945. The fossil collection of the British Museum was not available for study during the war, that is at the time when I was engaged in the study of the Illinois fossils. In treating the subject I was, therefore, obliged to accept as correct existing descriptions and figures of European Anthracomarti. This, as we shall see, led to serious errors which could not be foreseen at the time, but which I am fortunate enough to correct now. The collection of the British Museum, which was sent to me in 1946, contains numerous, excellently preserved specimens which, moreover, are much more complete than any specimens of the species of Anthracomarti, found in America. The present account

contains descriptions of many, previously quite unknown structures. Already Pocock was able to give a correct interpretation of some of the lines visible on the same surface of a specimen, although properly belonging to its opposite surface. But only excellent preservation of both surfaces of the same fossil specimen made it possible to distinguish the dorsal from the ventral lines and to give simple rules for their recognition in the tangle of lines on a single surface. It became possible to establish the correlation between the dorsal and ventral intersegmental lines and consequently to arrive at a correct interpretation of segments, the problem of segmentation being of first importance for the understanding of evolutionary trends, but one beset with dangerous pitfalls when approached without the safeguard of sufficient evidence.

The whole story of the growth of our knowledge of the Order Anthracomarti is a sad, but illuminating example of errors committed in attempts to interpret pictures presented by visible structures of incomplete fossil remains of animals long since extinct, by comparing them with structures of now living animals belonging to other orders. Since the development of this growth of our knowledge is interwoven with the discovery of other fossil Arachnida, namely Ricinulei, Trigonotarbi and Architarbi, the account of it is best presented historically.

The first Palaeozoic arachnid ever discovered, was a scorpion, described by Corda in 1835 under the name of *Cyclophthalmus senior*. Two years later, in 1837, W. Buckland described as beetles two fossils found by W. Anstice in England. One of these Buckland named *Curculioides ansticii*. It is now regarded as the type of the Genus *Curculioides* of the Order Ricinulei. The other fossil Buckland named *Curculioides prestvicii*. It is now regarded as the type of *Eophrynus prestvicii*, the first representative of my new Order Trigonotarbi. H. Woodward recognized its arachnid nature in 1871 and proposed for it the Genus *Eophrynus* coined by him with the special purpose of emphasizing its supposed affinity to that group of Recent Arachnida, which was usually regarded as a Suborder of the Order Pedipalpi, but which Millot and I have raised independently to the rank of an Order and which appears in my classification under the name of Phrynichida. Its affiliation with the Anthracomarti was first suggested by Karsch, in 1882, who proposed in that year the Order Anthracomarti for the inclusion of three genera, *Architarbus*, known since 1868, *Anthracomartus*, just described by Karsch, and *Eophrynus*.

Karsch placed his *Anthracomartus* with Scudder's *Architarbus* in the Family *Architarbidae*, regarding the two genera as closely related to each other. Scudder, who established the Genus *Architarbus* in 1868, included in his Family *Architarbidae* in 1890 not only *Architarbus* and *Anthracomartus*, but *Geraphrynus** and *Kustarachne* as well. Haase in the same year, 1890, removed the genera *Anthracomartus* and *Eophrynus* into the Order Opiliones, and the Family *Architarbidae* in which he retained only *Architarbus* and *Geraphrynus* into the Order Pedipalpi. Haase placed the Genus *Phalangiotarbus* in a different Suborder from the *Anthracomarti* also in the Order Opiliones. Pocock in 1902 established the relationship between the genera which he united in the Order *Phalangiotarbi*. At the same time he envisaged the classification which he developed in 1911 and which I followed with minor modifications up to the present.

The first representative of the Order *Anthracomarti* as emended in the present paper was discovered in Belgium. It was declared by L. G. de Koninck to be a hitherto unknown decapod Crustacean. Woodward described and figured it in 1878 under the name of *Brachypyge carbonis*, accepting de Koninck's diagnosis as correct. At that time *Anthracomartus* was not yet discovered. Karsch's paper appeared in 1882. The arachnid nature of *Brachypyge* was first recognized by Scudder in 1885. He synonymised the Genus *Brachypyge* with *Anthracomartus*. Pocock restored the Genus *Brachypyge* in 1902. Fritsch considered the original drawing as being rather fanciful. He says on page 42 of his *Palaeozoische Arachniden*, published in 1904: "Da die Figur Woodwards den Eindruck macht, dass sie vom Zeichner stark verschönert wurde . . .", but as later photographs made by Pruvost of the type specimen show, the original drawing was remarkably true to nature. Pruvost gave in 1930 a reconstruction of both surfaces of the abdomen, but his interpretation of the intersegmental lines is not free from error, as will be shown later, in the discussion of the species.

In the year 1882 H. B. Geinitz described a new fossil from the Coal Measures of Zwickau in Germany. He named it *Kreischeria wiedeii*. It is still known under that name, although Geinitz thought that it was a pseudoscorpion and placed it in that Order. It was not until 1890 when E. Haase pointed out Geinitz's error and placed

* As I have shown in 1913, the Genus *Geraphrynus* is a synonym of *Architarbus* because the type of *G. carbonarius* is a specimen of *Architarbus rotundatus*. (See my Monograph, p. 125).

the genus between *Anthracomartus* and *Eophrynus* in the Suborder Anthracomarti. We now know that it is closely related to *Eophrynus*.

In the same year, 1882, Karsch published his important discovery of a new fossil for which he proposed the Genus *Anthracomartus*, and the Order Anthracomarti. Since *Anthracomartus völkelianus*, described by Karsch in that paper, is the genotype and has been besides used by Karsch himself for the erection of his new Order Anthracomarti, it is of the greatest importance that we should be in possession of exact knowledge of the characters of the type specimen. Unfortunately this is not the case. As may be seen from the following account of the facts pertaining to this subject, our knowledge of the characters of the type is worse than inadequate. Karsch states in his paper that he based his description of the species on a study of several specimens collected by Völkel in Silesia. He did not designate any of these specimens as the Type, nor did he give the exact number of specimens, but referred to them simply as "a small number all apparently belonging to the same species" ("eine kleine Anzahl . . . mir zur Bestimmung übermittelter Arthropodenreste, die alle einer und derselben Form anzugehören scheinen." p. 556). According to his further statement, only one of these specimens represented the *dorsal* surface and is shown on Plate XXI in Figure 2. All the other specimens, according to Karsch's statement, showed the *ventral* surface and one of these was rendered in Figure 1 on the same Plate. Curiously enough, Karsch was misled in his interpretation of the two surfaces by the presence of a clear impression of the anal operculum on the surface which he considered to be ventral for this reason. His mistake was pointed out by Haase in 1890, who proved that Karsch's Figure 1 represents the dorsal and not the ventral surface notwithstanding the impression of the anal operculum, while Figure 2 shows the ventral and not the dorsal surface. Therein Haase was quite right and Karsch's mistake is easily understood and pardoned if one considers that no other related species were known at that time and that *Brachypyge* was still supposed to be a crab. *What remains not certain is the identity of the type specimen.* Haase states that he examined both specimens, the one shown by Karsch in Figure 1 and the other in Figure 2, and that his (Haase's) own Figure 9 on Plate XXX is a magnified drawing of the specimen shown in Karsch's Figure 1. But Haase's Figure 9 is in many respects different from Karsch's Figure 1. To emphasize this fact I have made photographs of both, enlarging them so that they would be of the

same size for easier comparison. These photographs are shown side by side in Figures 192 and 193. The original figures were in both cases drawings and not photographs. Were they made from the same specimen ? and if so, which drawing represents the fossil correctly ? Karsch's figure, although misinterpreted by him, shows the dorsal surface of a typical anthracomartid, as may be seen from its comparison with several species described in the present paper further down. Behind the carapace a large tergite is visible, which, as I shall show below, represents the fused second and third tergites. This plate is followed by five median tergal plates separated by almost straight intersegmental lines, even the last one being only gently recurved, and all with a double outline. Behind these plates, the plate with the impression of the anal operculum is clearly visible. This is the penultimate tergite, but the last tergite is not shown, nor are any marginal fields figured, although the submarginal fields are well outlined. The place normally occupied by the marginal fields is represented as an unsegmented border, but has a width comparable to that which would have been correct for marginal fields. Of the two longitudinal lines which normally separate the submarginal from the marginal fields, only the one on the left side of the drawing is visible and is shown in its proper position, i.e. about equally distant from the edge of the abdomen and the edge of the median tergal plates. The inner edge of the unsegmented lateral band occupies the normal position in which one would find the ventral longitudinal line separating the sternites from their marginal fields, superimpressed on the dorsal surface. The two longitudinal lines enclosing between them the median dorsal plates, are shown to be gradually converging, as should be. The carapace is shown with almost parallel sides and an almost transversely truncated front. On the left side of the specimen an almost complete leg, presumably the fourth, is figured.

Now turn your attention to Haase's Figure 9 reproduced in Figure 193. He states that it is a drawing made from the same specimen, yet it is much less typical of the more common species of *Anthracomarti*. The anterior intersegmental lines are fairly straight, but the posterior three lines are increasingly strongly convex, resembling rather ventral than dorsal lines and reminding one of the very unusual condition found in Pruvost's *Anthracomartus denuiti*. The two longitudinal lines enclosing the median tergal plates, are parallel as far as the middle of the tergite marked by Haase as the VIth, whence they converge strongly, so that at the level of the anal oper-

culum they are separated from each other by less than half of their original distance. The carapace is represented with evenly curved sides converging almost to a point in front, with a deep longitudinal crack somewhat to the left of the median plane. A transverse line is figured in front of the posterior edge of the carapace. Haase calls the narrow strip between the two the "posterior thoracic plate" ("hintere Thoracalplatte"), but from what we shall see later, this strip undoubtedly represents the impression of the anterior tergite, concealed under the posterior end of the carapace. Behind the carapace Haase figures a distinctly procurved intersegmental line and calls the short segment thus formed, the first dorsal plate ("die erste Rückenplatte"). This is definitely an error of interpretation. The curved line belongs to the ventral surface of the animal and the segment in question is the second sternite superimpressed over the large tergal plate, which I designate as representing tergites 2 + 3. The posterior end of Haase's figure is also confusing, showing a circle around the anal operculum, presumably due to superimpression of ventral over dorsal lines. In his diagrammatic drawing this circle is omitted from the dorsal surface shown in Figure 8 on Plate XXX. Finally, no leg is shown in Haase's Figure 9.

Karsch gives only *average* measurements. According to him all his specimens were ca. 18 mm. long. Haase gives no measurements at all. The total length of the specimen shown in Karsch's Figure 1, when the stated magnification of the figure is accounted for, comes to fully 23 mm., i.e. considerably more than the average length mentioned above from Karsch's own statement. Haase states that his figure is twice the size of the original. This makes the size of his specimen, shown in figure 9, not 23 but 20 mm. The size is, therefore, not of much help in determining whether Haase's specimen was really the same as that which Karsch figured in his Figure 1. It may have been some other specimen of the same batch. The only character which both figures have in common, is curiously enough the segmentation of the abdomen. I say "curiously enough," because Haase thought that he discovered the first tergite, overlooked by Karsch. But, as we have just stated, he mistook the second sternite for the first tergite. But both figures, Karsch's and Haase's, when properly analyzed show the same number of segments. This number, ten, is typical of all *Anthracomarti* as emended here and makes the Families *Pleomartidae* and *Coryphomartidae*, proposed by me in 1945, synonyms of *Anthracomartidae*.

In view of the evidence which I have discussed above, the specimen shown in Karsch's Figure 1 (and not the one shown in Haase's Figure 9) must be regarded as the Type of the species and of the genus. Whether Karsch's Figure 2 represents the ventral surface of an *Anthracomartus*, seems to me very doubtful. Karsch himself only assumed the identity of the two ("Die Identität beider Reste . . . vorausgesetzt"). His figure does not resemble the ventral surface of any species of the genera related to *Anthracomartus*. Only reexamination of the original specimen can solve the problem as to which group of Arachnida that specimen belongs.

By the time Haase's paper appeared in 1890 a number of fossil Arachnida were discovered and described in Europe and in America. Haase's classification appeared in the same year with Scudder's, but neither of them was satisfactory. The first comprehensive work on Palaeozoic Arachnida was published by A. Fritsch in 1904. By that time our knowledge of Recent Arachnida was considerable and the list of arachnologists included many a celebrated name. Yet Fritsch's book shows a distinct lack of knowledge of contemporary zoological and arachnological literature. It suffers badly from fanciful interpretations of structures visible on the surface of fossil specimens as structural parts of the fossils themselves. Thus he describes and figures two pairs of "genital appendages" in *Arthrolycosa*, *Protohylycosa*, *Geralycosa*, *Promygale* and *Eopholcus*. Then on page 26 he expresses the opinion that these appendages correspond to the first two pairs of spinnerets of Recent spiders ("Daraus ersieht mann dass die Genitalanhänge den ersten 2 Paaren der Spinnwarzen der jetzigen Spinnen entsprechen und das 3 Paar auch noch vorhanden war."). But not only have the spinnerets of spiders nothing to do with "genital appendages," Fritsch's *Promygale* is not a spider, but an anthracomartid, and since no anthracomartid has either spinnerets or genital appendages it is difficult to understand, *what* were the structures which Fritsch figured. Fritsch described also four posterior, segmented abdominal appendages in *Petrovicia* ("vier gegliederte Anhängsel"). They are probably nothing else than fractured posterior spines. Fritsch's classification is a step back by comparison with that of Haase and was soon superceded by that of Pocock.

Pocock possessed extensive knowledge of Arachnida in addition to his thorough zoological training. In his papers on fossil Arachnida he contributed a great deal to the elucidation of their structure and relationships. His interpretations are usually correct, except

where they deal with the problem of segmentation, inasmuch as he was influenced by Ray Lankester's brilliant theories some of which proved later to be erroneous. Pocock's Carboniferous Arachnida published in 1911 is a work which shows his remarkable grasp of the subject. Some of his errors, especially such as were caused by lack of first-hand acquaintance with American fossil Arachnida, were corrected by me in my Monograph in 1913. The paper of Hirst, published in 1923 and dealing with Devonian Arachnida added considerably to our knowledge of that group which I now segregate in the Order Trigonotarbi. But in my paper on Palaeozoic Arachnida of Illinois, published in 1945, I still placed them in accordance with Pocock's classification in the same Order with the Anthracomarti. As already stated I wrote that paper without first-hand acquaintance with the European fossil Arachnida, and the errors contained in it are comparable to those in Pocock's great monograph. Much as that is lamentable, there was no other way of approaching the subject than by assuming the correctness of published descriptions. These errors are now eliminated by the present investigation which, let us hope, clears up for good many moot points of structure and classification.

Interpretation of Abdominal Longitudinal and Transverse Lines

A common feature found in Anthracomarti is superimpression of dorsal and ventral lines on the same surface. Some of these lines have been satisfactorily explained. Others still need identification of their nature before the structure of the abdomen can be correctly understood. This we shall attempt to do now.

It is well known that the dorsal surface of the abdomen is longitudinally divided by two pairs of lines into five rows of plates. But in many cases one can see on each side of the abdomen an additional longitudinal line between the edge of the abdomen and the outer dorsal line. This supernumerary pair of lines was properly regarded as being ventral, and not dorsal, in position, because in many specimens it appears only on the ventral surface. It is shown in its proper place in Pocock's figures of *Maiocercus* and *Anthracomartus*. But the interpretation of the fields formed by this line on the ventral surface of the abdomen, with exception of the postanal one, is incorrect. The latter was properly interpreted already by Haase as forming part of the last dorsal tergite, turned under on the ventral surface where it is separated from the corresponding sternite by the ventral line under discussion. This interpretation was accepted by everybody and may

be best understood from Figures 36 to 39, in which the dorsal lines are shown in red, the ventral ones in black. But does this interpretation apply to the other fields of the ventral surface, situated between the edge of the abdomen and the line in question? And if so, is the ventral surface restricted to the central row of undivided sternites? or if not, do the ventral fields forming the so-called pleural plates really belong to the ventral surface? Pocock seems to have accepted the latter alternative. On page 62 he says: "in no specimen that I have seen is the ventral surface exposed fully from below. In every case where the sternal plates are well shown it is their inner surface that is exposed—that is to say, the organism is split in two in such a way that the dorsal area is seen from below and the ventral area from above." "The Anthracomartidae are sharply distinguished from the Eophrynidae and from the Anthracosironidae . . . by the separation of the pleural plates into an outer and an inner moiety by sulci, which are apparent upon the ventral as well as upon the dorsal surfaces." On page 59, in the key to genera, Pocock speaks of the "pleural laminae of the first, second, third, and fourth sterna." Yet I am unable to find in any of his papers a definite statement as to whether these pleural laminae are portions of the sternites, or of the tergites as in the case of the postanal one, which Pocock interprets as a turned under portion of the last tergite, in conformity with Haase's original suggestion.

The question as to the real nature of these laminae can be settled only by a study of specimens in which the line in question appears only on one surface, or by the line of splitting between the two surfaces when they happen to be slightly displaced in relation to each other. Both cases are fortunately represented in the collection of the British Museum. Perhaps the most illuminating of these is represented by a specimen of *Cryptomartius priesti*, numbered as In. 31264 and shown photographically in Figures 204 and 205. The specimen consists of two pieces, both of which showed originally only the dorsal surface and that without the supernumerary lines, as will be clearly seen from Figure 204. The appearance of the piece shown in Figure 205 after its preparation, made me think that here the dorsal surface was impressed on mineral substance which filled the original cavity of the abdomen and concealed from view the ventral inner wall of it. Proceeding on this assumption and feeling justified in removing part of the fossil, equally well visible on the other piece, I removed with the aid of a chisel most of this material on the sides

and in the posterior half of the abdomen. This operation exposed the inside of the ventral body wall to view as shown in Figure 205. The lateral line separating the sternal plural laminae, or as I call them—the sternal marginal fields, is now plainly visible. On the anterior remnant of the mineral mass we still can see the dorsal intersegmental lines.

The collection contains several specimens in which the two surfaces are slightly shifted. One of these cases is shown in our Figure 34 in which the dorsal lines are represented in red and the ventral ones in black. Such displacement is possible only if the dorsal and ventral walls are easiest separable along the edge of their union, where they are bound presumably by either a thin membrane or at any rate by less rigid chitin. Thus it may be considered as definitely proven that only the last tergal plate extends to the ventral surface and that the other ventral plates are true marginal fields of sternites.

The true nature of the intersegmental lines and of the corresponding segments themselves is best understood by superposition of the two surfaces of the same specimen. Such superposition is shown in Figure 35 in red and black and the two surfaces of the same specimen are shown also separately in Figures 53 and 54. In examining these three figures we see at once that here is one tergite less than there are sternites. This tergite is exceptionally long and corresponds to the second and third sternites, the first sternite being represented by the anterior tergite and the fourth and following sternites coinciding by their lateral edges with the tergites. The conclusion is inescapable, that *the long tergite is the result of a fusion of the second and third tergites.*

The existence of the first tergite was not known, or at least not definitely established before. Its existence may be now regarded as absolutely certain. A number of specimens show this tergite. In specimen In. 31264 of *Cryptomartus priesti* already alluded to above in connection with the true nature of the ventral lateral fields, the first tergite is fully exposed (Figure 204). The specimen may have been an exuvium, or may have been dismembered through rotting, before it became fossilized. It shows clearly the thickened anterior edge of the first tergite. It is due to this edge that in specimens in which the first tergite remains concealed under the carapace, its outline is still visible as a transverse impression across the posterior end of the latter. Moreover, the shape of the tergite and of its thickened edge leave no doubt as to the juncture of the abdomen with the carapace: it *occupied the full width of the first tergite.*

With all these facts in mind it becomes possible to reconstruct the structure of the abdomen in all known species of *Anthracomarti*. The most interesting result of this is the fact that it is always composed of ten segments, the second and third segments have their tergites always permanently fused as a single plate and the tenth segment has never lateral fields on its dorsal or on its ventral surface. The first segment has always a triangular sternite and a tergite with a thickened anterior edge for attachment of the membrane connecting it to the carapace. The ninth segment is strongly recurved to accommodate the tenth segment between its two arms and its tergite shows a distinct tendency toward a fusion between the median plate and the two triangular submarginal ones, resulting in such a case in a single, hexagonal plate. This is noticeable in *Brachypyge* and *Coryphomartus* as shown in Figures 60 and 59. When I first studied the latter in 1913, I was unable to understand its segmentation, the tangle of visible lines was great and the resulting figure unlike anything else among the *Anthracomarti*. This time I was able to reexamine the specimen. After cleaning once more its surface I could find without difficulty the intersegmental lines among the confusing lines of folds in the matrix. Figure 191 shows a photograph of the specimen as it now appears. The first tergite is the only feature not visible, but there is no doubt in my mind that it is concealed under the carapace. Figures 60 and 61 are reconstructions of the dorsal and ventral surfaces of *Brachypyge carbonis*. Both figures were drawn by me over photographs of the original single picture accompanying Woodward's paper. The only difference is that I separated the ventral from the dorsal lines. In the original figure they appear on the same surface. The missing lines I introduced as broken ones, to indicate that they are not visible on the original figure. A comparison of these two figures with Pruvost's photograph and reconstruction published in 1930 (p. 211, Fig. 8 and Plate XI, figures 1 and 2) shows at once how remarkably near to nature Woodward's figure is. It also shows that Pruvost mistook the ventral lines for dorsal ones, for he shows both on the dorsal surface and he missed the composition of the second visible tergite of two completely fused ones. The same applies of course to Pruvost's earlier reconstruction of *Majocercus celticus*, published by him in 1919 under the name of *Maiocercus orbicularis* (page 360, figure 44). When properly reconstructed the lines and segmentation appear as in Figures 62 and 63. The segmentation of *Anthracomartus völkelianus* is shown in Figure

55 as reconstructed from Karsch's Figure 1. Figure 56 shows my reconstruction of Fritsch's *Promygalobobemica* from his own figure on Plate 15, but with omission of the distal portions of the appendages and of the line across the ninth tergite, which in my opinion is not a part of the creature's own structure. Figure 57 is my tentative reconstruction of *Anthracophrynus tuberculatus* Andrée. Unlike Andrée himself and other interpreters of this fossil, I believe that the structures in front of the first visible tergite, marked as the 4th in my figure, are not remnants of the carapace, but of the anterior tergites, as indicated by dotted lines. Ammon's *Anthracomartus palatinus* described and figured by him in 1900 was variously, but not correctly interpreted by him, Pocock and Pruvost. The original figure of Ammon is photographically reproduced in Figure 194. I suspect that the drawing is not quite true to nature and that there should be no such wide separation between the carapace and the abdomen, because the posterior end of the former shows clearly the first tergite concealed under it. The two segments with procurved edges, situated on the median tergal plate 2 + 3, are the second and third sternites. The line immediately behind the anal operculum probably does not belong to the animal and may be the result of an optical illusion due to the convergence of the dorsal lines. Finally the outer of the two curved lines running parallel to the edge, belongs to the ventral surface. The anal operculum, naturally, also belongs to the ventral surface. The result of this reconstruction makes *Anthracomartus palatinus* remarkably similar to *Pleomartus trilobitus* shown in Figure 58, with the slight difference in the shape of the carapace. In my paper of 1945 I gave wrong numbering of the tergites. Reexamination of the Type and other specimens in the U. S. National Museum has convinced me that the first tergite is present, is exposed to view and plainly visible as shown photographically in Figure 190.

The discussion of other points in the anatomy of *Anthracomarti*, such as the respiratory and reproductive system, will be found in the Introduction to this paper.

Remarks Concerning Genera Originally Referred to or Considered To Be Related to *Anthracomarti*

The Genus *Brachypyge* was established in 1878, the genus *Maiocercus* in 1911 for a species originally described by Howard and Thomas in 1896 under the name of *Eophrynus carbonis*. Pocock proposed the Family *Brachypygidae* for these two genera in 1911,

because of their festooned abdominal edge. Pruvost recognized this family as late as 1930 in opposition to my opinion that the character on which the family is based is not of familial rank. I expressed this opinion in 1913 and still consider it valid. We know many Arachnida in which this character has only generic value. We also know some spiders in which the females have a more or less festooned, often spined abdomen, while the males do not exhibit anything of the kind or in a very reduced degree, as in the case of some Recent *Argiopidae*. Pruvost puts stress on a character which was not known to Pocock because of the incomplete preservation of his specimen which lacked the cephalothorax. The character is derived from the structure of the carapace which Pruvost considers to be segmented. He also speaks of the subdivision of the lateral (pleural) tergal plates into three fields, an outer, a median and an inner one. On page 357 of his Dissertation published in 1919, Pruvost states: "1°. Le céphalothorax est segmenté, construit sur un type identique à celui des Eophrynidés; 2°. Les segments sur la face dorsal de l'abdomen sont divisés en lames tergaes et lames pleurales, ces dernières subdivisées en trois parties (externe, moyenne, interne)." Neither of these characters is valid. The carapace of *Maiocercus* is not segmented, but only sculptured. The difference between sculpturing and segmentation is explained in the Introduction to this paper. The subdivision of the pleural laminae is an illusion due to superimpression of ventral over dorsal lines as explained above. The correctness of the first objection is substantiated by the condition of the specimen of *Aphantomartus* described by Pocock. Although this genus belongs to the *Trigonotarbidæ*, it has a sculptured carapace similar to that of *Maiocercus*. It happens that Pocock's specimen was either an exuvium or was disrupted before fossilization. Its carapace (Pocock, 1911, Plate III, figure 6) is figured as lying at an angle to the abdomen and yet preserving its identity as a single plate.

The Genus *Maiocercus* Pocock was recognized by me in 1913, but was synonymized with *Brachypyge* by Pruvost in 1930. I think it may be retained because of the markedly different proportions of the abdomen. Moreover, its carapace is known, while that of *Brachypyge* remains to be discovered. It is, of course, possible that *Maiocercus* will have to be eventually synonymized with *Brachypyge*, if the carapace of the latter will prove to be similar to that of *Maiocercus*. The proportions and structure of the carapace are more constant and therefore more important characters than those of the abdomen, as

experience with other groups of Recent Arachnida shows. For the present the retention of the genus has at least practical value.

The Genus *Promygale* Fritsch seems to me to be a synonym of *Pleomartius*; judging by the published figure the carapace of its type species is much wider than long. The other two species of *Promygale*, namely *P. rotundata* and *P. elegans* possibly belong to the Genus *Anthracomartius*. Fritsch mentions the presence of eyes and of genital appendages. His descriptions are fanciful and not reliable. None of the *Anthracomarti* known to me from actual specimens show the slightest trace of eyes, nor of any structures that could be interpreted as genital appendages. Ammon shows ocelli in his figures 2 and 3 of *Anthracomartius palatinus*, but adds that the nature of the visible structures is not certain ("doch ist die Sache nicht ganz klar.") and suggests that they may be not eyes, but granules.

The genera *Cyclotrogulus*, *Stenotrogulus*, *Hemiphrynus*, *Vratislavia* and *Petrovicia*, all proposed by Fritsch, must be regarded at present as *incertae sedis*. *Stenotrogulus* seems to be almost certainly a Trigonotarbid and it is possible that Guthörl's *Eophrynus waechteri* is identical or at least co-generic with Fritsch's (23) *Stenotrogulus salmii* (Stur). If that will prove to be the case, my Genus *Phrynomartius*, proposed by me in 1945 for Guthörl's *E. waechteri* will become a synonym of *Stenotrogulus*. The genera *Cyclotrogulus*, *Hemiphrynus* and *Vratislavia* may also belong to the Order Trigonotarbi, but in their case the affiliation is much less certain. Finally *Petrovicia* may be an *Anthracomartid* if judged by Fritsch's reconstruction, but the presence of four posterior spines suggests that it may be related to *Eophrynus*.

The Genus *Eotrogulus* Thevenin, listed by me in 1913 among the *Anthracomartidae*, seems to be an opilionid. The photograph published by Thevenin resembles somewhat the Haptopoda. Only careful reexamination of the type specimen can settle the question of its affiliation.

The Genus *Adelocaris* Packard listed by me erroneously in 1913 among the *Eophrynidae*, is not an arachnid (see Fritsch, 23, p. 54).

The Genus *Anthracophrynus* Andrée, proposed in 1913 and therefore not included in my Monograph of that year, was based on the characters of a single, not complete and not very well preserved species, *A. tuberculatus*. According to Andrée the fossil is represented only by a fraction of the dorsal surface of its abdomen and by a portion of what he interpreted as the remains of the carapace. The

name was chosen to indicate that the visible structures of the fossil resemble in some respects those of *Anthracomartus* and in other respects *Eophrynus*. No photograph of the specimen had been published and the drawing accompanying the paper is not very distinct because of the comparatively coarse grating used in its printing. In addition to this drawing Andrée gave a diagrammatic reconstruction of the abdomen. According to this reconstruction the abdomen consisted of only seven segments and the tergites were divided into five rows as in *Anthracomartus*. The chief distinction of the fossil, according to Andrée, is the presence of paired tubercles on each median tergal plate. Waterlot who was unable to study the original specimen, came to a different opinion from that of Andrée, on the basis of the description and figures published by Andrée. In his Thèses published in 1934 Waterlot suggests that the longitudinal lines interpreted by Andrée as the lines separating the marginal from the submarginal fields are possibly mere chance folding of the integument and have no structural value. He points out that if his suggestion were proved to be correct, then *Anthracophrynus* would present all the distinctive characters of the Genus *Trigonomartus* as the latter was defined by me in 1913, and would become a synonym of the latter. The original specimen was not available to me for reexamination. Consequently my opinion is also based only on a study of Andrée's description and figure. Yet it seems to me that the lines in his drawing are too regular and too definitely in the place which should be occupied by them if they are what Andrée supposed them to be, to be waived aside as artifacts. Nor does Andrée's reconstruction appeal to me. The shape of the abdominal piece shown in the drawing is so unusual that it could be interpreted only as the result of considerable distortion, or else as a much smaller remnant than accepted by Andrée. In the first case one would have to expect the presence of blank, wedge-shaped or triangular spaces of the matrix filling out the spaces between torn and rent asunder portions of the body. Stretching of the body wall without tearing is not probable and the drawing does not present such a picture. For this reason I am inclined to accept the second alternative, namely that the preserved piece of the abdomen represents a much smaller portion of it than assumed by Andrée. I think that the portion which he interprets as a piece of the carapace, is in reality a portion of that tergite which corresponds to the fused second and third tergites of *Anthracomarti*. If we add in front of it the narrow first tergite which, as I have shown above, is often con-

cealed in Anthracomarti under the carapace, we get a picture of segmentation typical of all Anthracomarti (Figure 57). However, my own reconstruction is only tentative and I do not include the genus in the key published below.

Characters of the Order Anthracomarti, emended

Carapace entire, without a doublure, smooth or sculptured. Eyes wanting. Abdomen broadly joined to the cephalothorax, dorsally by the full width of its first tergite, ventrally by the sides of the first triangular sternite wedged in between the fourth coxae. The abdomen is composed of ten segments (not counting the anal operculum), each segment with a tergite and a sternite, but the second and third tergites are fused without a trace of the intersegmental line, so that only nine plates can be counted. First tergite entire, often concealed under the carapace. Last tergite also entire and so folded that its posterior half is ventral in position and is bordered in front by the posterior edge of the anal sternite and on the sides by the marginal fields of the ninth sternite. Occasionally the intersegmental line between the penultimate and the last tergite is wanting, in which case the single plate thus formed has the shape of an hour-glass. The tergites situated between the first and the last are subdivided into five plates each by two pairs of longitudinal lines, namely a median plate, a pair of submarginal and a pair of marginal plates. The submarginal plates of the tergal plate which may be best numbered as $2 + 3$, are triangular, as are the submarginal plates of the penultimate tergite. The latter are occasionally completely fused with their median plate which then is hexagonal in shape. The first and tenth sternites are entire, those between them are subdivided into three fields each by two longitudinal lines parallel to the outer edge of the abdomen and situated between it and the outer dorsal longitudinal line when the latter happens to be impressed on the same surface with the former, the ventral marginal fields being always narrower than the corresponding dorsal ones. Anal operculum on the tenth sternite. It has two valves, a larger anterior one and a smaller posterior one.

Chelicerae three-jointed, the third joint presumably retrovert. Chelical coxae wedged in between the pedipalpal coxae, in the same plane with the latter and the pedal coxae. All coxae movable. Pedipalpi six-jointed, pediform. Legs seven-jointed, their trochanters single-jointed, their tarsi ending in a pair of claws on an onychium. Sternum long and

narrow. Mouth ventral, between the first pedal coxae. Three pairs of book-lungs situated on the second, third and fourth sternites, to the inside of apodemes serving for the attachment of respiratory muscles. Sexes separate. Genital opening in both sexes near posterior edge of second sternite leading into a genital atrium, with a pair of sperm vesicles in the male and a pair of sperm receptacles in the female in a depression on the third sternite and paired openings on the second sternite. Carboniferous and Permian.

Family ANTHRACOMARTIDAE

(= *Anthracomartidae* + *Brachypygidae* + *Pleomartidae* +
Coryphomartidae)

This is the only family and is therefore recognizable by the characters of the Order. Pocock's family *Brachypygidae* and my families *Pleomartidae* and *Coryphomartidae* are not distinguishable from the *Anthracomartidae* except by generic characters. These are the shape, structure and relative proportions of the carapace and of the abdomen. Whenever the carapace is well preserved, the separation of the genera is a simple matter. The sculptured carapace of *Maiocercus*, the smooth, triangular carapace of *Coryphomartus*, the crested carapace of *Cryptomartus* are very distinct. Greater difficulty is encountered in the separation of the three allied genera. *Anthracomartus*, *Pleomartus* and *Cleptomartus*. In all three the carapace is flat and devoid of sculpturing, leaving only its shape and relative proportions for comparison and differentiation. The existence of variations may be expected *a priori*; some variations are discernible even in the comparatively few specimens available. The distinction of the genera is based on the value of the mean of variations determined by measurements of several specimens. The distinction may disappear if the limits of variation were to overlap. In that case the genera *Pleomartus* and *Cleptomartus* would have to be synonymized with *Anthracomartus*, or at best retained as subgenera. But the status of the Genus *Anthracomartus* is uncertain, as explained above in the Introductory Remarks to the Anthracomarti. Meanwhile the transversely rectangular shape of the carapace of *Pleomartus* with its ratio of length to width in the type amounting to 1:1.4 and almost of the same value in the other specimens, clearly separates it from the other genera in which it is about 1:1 in *Cleptomartus* and 1:1.1 in *Anthracomartus*. The separation of these last two genera is still more difficult, but is somewhat aided by the difference in the shape of the carapace. The cara-

pace of *Anthracomartus* is figured by Karsch as being almost square, with rounded anterior corners and slightly concave front. The carapace of *Cleptomartus* is appreciably narrowed in front, with an evenly convex anterior edge. Pocock used for the distinction of species the ratio between the length and the width of the median penultimate (my ninth) tergal plate. This character is good, but does not have generic value. I have measured the ratio between the length and the width of the entire central area formed by the median plates of the tergites which I call the fourth to eighth, and have found this character very valuable, but also of only specific value. In combination with other characters these ratios may be very useful. Thus in *Pleomartus* the ratio of the central area is 1 : 1.03, in *Coryphomartus* 1 : 1.70, in *Anthracomartus* (as derived from measurements of Karsch's figure) 1 : 0.82, in *Cleptomartus plautus* 1 : 1.1. In *Cleptomartus planus*, the other species of the genus, it is practically the same as in *Anthracomartus*, but the carapace is distinctly narrowed in front. In other words, *Cleptomartus plautus* can be differentiated from *Anthracomartus* more easily by the ratio of its central area, *Cleptomartus planus* by the shape of its carapace.

Key to Genera of Anthracomartidae

1. Lateral edge of abdomen festooned. Carapace sculptured 2
- Lateral edge of abdomen evenly convex. Carapace not sculptured 3
2. Carapace not known. Abdomen longer than wide. Median tergal area twice as long as wide, the ratio of its length to its width ca. 1 : 0.5. Median tergal plate of the ninth somite (penultimate) longer than wide, sometimes fused with its triangular submarginal plates into a single, hexagonal plate, without a trace of the dividing lines. Genus *Brachypyge* Woodward.
- Carapace subtriangular, distinctly sculptured. Abdomen somewhat wider than long. Median tergal area almost as wide as long, its ratio 1 : 0.93. Ninth median tergal plate always distinct, wider than long, with equally distinct triangular submarginal plates. Genus *Maiocercus* Pocock.
3. Carapace an equilateral triangle with slightly concave sides, flat and smooth. Median tergal area considerably longer than wide in ratio of 1 : 0.7. Triangular submarginal

- plates of the ninth segment (penultimate) fused with the median plate into a single hexagonal plate. Intersegmental line between the penultimate and the last tergal plates clearly visible. Genus *Coryphomartus* Petrunkevitch.
- Carapace not an equilateral triangle. Submarginal triangular fields of the penultimate segment distinct 4
4. Carapace high, with almost vertical sides converging anteriorly in a convex curve. The obliquely inclined front with a median, longitudinal crest extending over the cephalic portion and reaching the anterior edge of the carapace. In transverse section the crest is perfectly rectangular with square corners. Genus *Cryptomartus* Petrunkevitch.
- Carapace flat, with slanting sides, without a crest 5
5. Carapace much wider than long, with a ratio of length to width of 1 : 1.4, transversely rectangular with rounded anterior corners. Genus *Pleomartus* Petrunkevitch.
- The ratio of length to width of the carapace does not exceed 1 : 1.1 6
6. Carapace with sides converging anteriorly, anterior edge evenly rounded. Ratio of length to width of carapace 1 : 1. Genus *Cleptomartus*, new.
- Carapace with ratio of length to width 1 : 1.1, sides parallel, front transversely truncated and slightly concave, anterior corners rounded. Median tergal area longer than wide in ratio 1 : 0.8 (characters based on Karsch's figure). Genus *Anibracomartus* Karsch.

Genus *Anthracomartus* Karsch, 1882

Type *A. völkelianus* Karsch

The status of this genus has been discussed above and its characters given in the key as far as they can be derived from the original description of the type and its figure. Without a reexamination of the type specimen it is impossible to decide whether any of the species described under this genus by later investigators, really belong to it. Pending such reinvestigation the later species may be tentatively placed in the genera proposed here.

Genus *Pleomartus* Petrunkevitch, 1945Type *P. trilobitus* (Scudder) sub *Anthracomartus*

It is unfortunate that it is necessary to give here a new definition of this genus proposed by me in 1945. At that time it was impossible for me to reexamine the type specimen and I was misled by theoretical conclusions. Recently I reexamined the type and several other specimens. A photograph of the type is shown in Figure 190 and the segmentation of its abdomen in Figure 58. It will be seen that the latter differs from figure 30 on page 59 of the Palaeozoic Arachnida of Illinois by showing a tergite in front, which is omitted in figure 30. It differs also in the labelling of the following tergite as 2 + 3 instead of 1.

The Genus *Pleomartus* is represented in America by its genotype, of which at least twenty-two specimens are known, all from the same Upper Pottsville series, near Fayetteville, Arkansas. The Type is in the U. S. National Museum. It is described in my Monograph (1913). Ammon's *Anthracomartus palatinus* is probably a *Pleomartus*. Although Ammon states that the carapace is 7 mm. long and 6 mm. wide, his figure contradicts this statement: it shows a carapace fully one third wider than long. *Anthracomartus granulatus* Fritsch and *Promygalé bohémica* Fritsch seem both to belong to the Genus *Pleomartus*.

Genus *Cleptomartus*, newType *C. plautus* n. sp.

This genus is closely related to the two preceding genera with which it shares two characters of its carapace: the relatively short dorso-ventral axis and the obliquely slanting sides. It appears therefore distinctly flat. It is distinguished from *Anthracomartus* and *Pleomartus* by its convex anterior edge and the ratio of its length to its width. The abdomen does not present distinctive characters.

Two species belong to this genus. They may be distinguished as follows.

Median tergal area slightly wider than long. Angle formed by the eighth sternite is ca. 120° *C. plautus* n. sp.

— Median tergal area slightly longer than wide. Angle formed by the eighth sternite is ca. 90° *C. planus* n. sp.

It is possible that *Anthracomartus denuiti* Pruvost belongs to this genus.

Cleptomartus plautus n. sp.

The following 13 specimens in the collection of the British Museum belong to this species:

In. 15896—Type. Female.

In. 7884 and 7916 (dorsal and ventral surfaces of the same specimen)—

Paratype. Female.

In. 15884—Female.

In. 7920—Sex uncertain.

In. 15898—Sex uncertain.

In. 15857—Androtype. Male.

In. 18336—(Pocock's paratype of *A. priesti*) Male. Paratype.

In. 7915—Male.

In. 18334—(Pocock's paratype of *A. preisti*). Sex uncertain.

In. 18335—(Pocock's paratype of *A. priesti*). Sex uncertain.

In. 13956—(Pocock's paratype of *A. priesti*). Sex uncertain.

In. 15895—Sex uncertain.

In. 31251—Sex uncertain.

All these specimens come from the same horizon and locality, namely from the bed of nodular ironstone about 10 feet above the thick or 10 yard coal, Coseley, Staffs.

It will be noticed that four of the specimens referred by me to this species are Pocock's paratypes of his *Anthracomartus priesti*. None of his specimens were properly cleaned of extraneous mineral matter. As we shall see below, in the description of the two species of *Cryptomartus*, Pocock's description of their carapace is incorrect. The crest, on the presence or absence of which I distinguish the genera, escaped his notice because it is easily overlooked when the cavity of the carapace is filled with kaolin or other mineral, leaving only the edge of the carapace visible. I subjected all 13 specimens to careful examination and made all essential measurements needed for comparison. These measurements are given here for the sake of a record, but only the type is described in detail.

Description of the Type, In. 15896. Two pieces. Figures 81-83, 84, 85, 89, 216, 217, 221 and 223.

This is an exceptionally well preserved specimen shown photographically in Figures 216 and 217 as it appears on the nodule. The specimen is particularly interesting because it gives a clear idea of the general appearance of a typical representative of the Order

Anthracomarti. Pocock's figure of his *A. priesti* is a reconstruction, incomplete and in part erroneous. His figure of the dorsal view of *A. hindi* is also a reconstruction, an ingenious restoration of appendages on the basis of incomplete pieces belonging to different specimens. It is difficult to say whether the legs have the appearance and proportions given to them by Pocock. Figure 81 is a camera lucida drawing showing that the legs of at least this species were relatively longer and stouter than in Pocock's reconstruction of his *A. hindi*.

Piece *a* of the type shows the inside surface of the dorsal wall in both the carapace and the abdomen. Nevertheless the carapace appears concave and the abdomen convex, a common phenomenon in Anthracomarti, but one difficult to interpret. The carapace having been in life presumably hard, retained its shape, except for slight distortion. That it is its inside surface which is exposed to view, is proven by the fact that the first abdominal tergite appears overlying it, not concealed under it as would be the case if the exposed surface of the carapace were the outside one. The abdomen is evidently pressed in, appearing convex as in its natural state, and not concave as it should appear in a mold. The edge of the abdomen, composed of the row of marginal plates, is more or less flat. It is also flat on the piece showing the ventral surface of the abdomen, but the rest of that surface is concave as it should appear in a mold. Only two explanations of this peculiar phenomenon occur to me. Either the ventral wall was considerably harder than the dorsal one and remained convex while the dorsal wall was caved in in the process of fossilization, or else the individual plates of the dorsal surface were held together by soft, elastic membranes. This latter alternative seems to me to be the more probable one and explains not only the caving in of the dorsal surface, but also the wide shape of the lines separating the tergal plates. If, as Pocock assumes, the individual plates were "apparently welded together, though the sutural lines persist," such caving in of the dorsal wall, without rupture of any kind visible in the fossil, would be impossible.

The carapace is complete, but somewhat distorted by two transverse folds appearing as grooves, the anterior one across the middle of the carapace, the posterior one following the convex outline of the anterior edge of the first tergite. A deep groove separates the first tergite from the following one which is the fused plate of the second and third somites. This plate and the following one, which is the fourth tergite, are coarsely punctured and the fifth to eighth tergites have

each a transverse posterior row of similar punctures. The marginal plates are also clearly punctured, but the carapace is not punctured.

The proximal portions of all legs are raised above the level of the carapace. All four right legs are visible on the left side of the nodule and four legs on the opposite side, but of these only the fourth is complete. Many joints show the presence of coarse punctures. The dorsal surface of the animal, except for its carapace, was roughly granular in life. One also can see a pair of longitudinal folds on the patella of the third and fourth pair of legs, and a median longitudinal fold on the tibia. Similar folds may be seen on the first and second pair of legs, but they are much less distinct. The legs, like the rest of the specimen, show the inside surface, not a mold of the outside one. It is consequently difficult to decide whether these longitudinal folds correspond to external grooves or represent the space separating two longitudinal muscles which disintegrated and appear in the fossil as furrows on the sides of the fold.

Piece *b* shows the ventral wall of the fossil, viewed mainly not as a mold of its exterior surface, but as the inside surface, at least in the abdomen. The latter is complete except for a small piece on the right side, as indicated by dotted lines in Figure 89. The intersegmental lines are very sharp except in the anterior three segments which may be easily recognized by the presence of three, deep depressions usual in *Anthracomarti*. These depressions are sharply outlined. The surface of the sternites is coarsely punctate and must have been granular on the external surface in life. The anal operculum is very distinct, but the transverse line between the two valves is barely visible. The marginal plates are quite distinct. The line separating them from the median plates is straight, but the transverse line between the tenth sternite and the ventral portion of the tenth tergite is distinctly recurved. The cephalothoracic portion of piece *b* is convex and consists of a mixture of molds of coxal cavities, of the endosternite and of a couple of fossilized muscles. The second joints of both chelicerae are displaced, glossy, completely fossilized and of a different color from the matrix. They are shown in Figures 84 and 85 and can be seen also in Figure 221, where they are reproduced photographically. Viewed from in front they appear stouter in their middle than at the ends, are distinctly attenuated and diverge distally. In side-view they appear distinctly concave along their anterior edge. At the distal end of the left joint the two articulation points of the third joint are visible, but the joint itself is missing, nor is there any indica-

tion of a process on the visible joint in the place in which one would expect the immobile finger to be, if the chelicerae were chelate. In front of the chelicerae both pedipalpi are preserved as far as the ends of the femur. The cavity leading into the patella is turned straight up and is quite square as may be seen in the photograph. The inter-segmental membrane is fossilized as such and shows wrinkles. The right legs are complete and the tarsus of the third leg has a very distinct and long claw shown in Figure 82. A small onychium is present. The claw itself is curved and smooth. The fact that the onychium is attached to the ventral end of the tarsus bespeaks the presence of a pair of claws, although only one of the pair is preserved, because a single claw would be terminal and more or less centrally placed, as is the case, for example, in Recent Opiliones.

Measurements. Total length 10.7 mm. Carapace 4.3 mm. long, 4.3 mm. wide, flat, without eyes, evenly rounded in front, truncated behind. Abdomen 6.4 mm. long, 6.4 mm. wide on the level of the fourth (third visible) tergite where it is widest. Ratio of the length of the carapace to that of the abdomen 1 : 1.4. Median tergal area formed by the median fields of tergites 4 to 8 is 3.57 mm. wide in front, 3.14 mm. long in median line, but 3.30 mm. long if measured to an imaginary line tangent to the posterior corners of the area. The ratio of length to width of this area is therefore 1 : 1.1. The ninth tergite is 1.64 mm. wide in front, 1.07 mm. long in median line. Its ratio of length to width is 1 : 1.6. Length of second joint of chelicerae 0.80 mm. Leg formula

4	1	3	2
1.4	1.4	1.4	1.3

The difference in the length of the first and third legs is in the third decimal. The formula shows the remarkable uniformity of the legs, with a but slightly greater length of the fourth pair and a slightly shorter length of the second pair which is the shortest.

Legs	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	1.86	1.00	1.14	0.86	1.00	5.86
II	1.86	1.14	1.14	0.57	0.86	5.57
III	1.86	1.14	1.29	0.57	1.00	5.86
IV	2.00	1.14	1.29	0.57	1.00	6.00

A characteristic feature of the legs is the *greater length of all tarsi as compared with the metatarsi*.

The angle formed by the sides of the eighth sternite is ca. 120°.

The three depressions in the anterior portion of the abdomen, mentioned in the Introduction, are deep and with clean-cut edges.

The first depression which I have marked as A in all figures, and which belongs to the second sternite, represents the atrium (or uterus externus) and is more or less triangular. The anterior angle is about 90° , the posterior angles 45° each. There is a central, cup-like depression in the posterior region of the triangle. This depression is best visible when the specimen is examined from in front, because the mouth of the cup is directed forward. The triangular depression must have appeared in life from the outside as a triangular swelling of the ventral wall, with the apex directed forward. The second depression B, belonging to the third sternite, is procurved, more or less bean-shaped, with rounded ends, as wide as the triangular depression. The third depression C is considerably wider, but much shorter in its antero-posterior direction, so that it looks like a curved, narrow, long, transverse trough. The meaning of the third depression is difficult to guess. As explained in the Introduction, the anterior two depressions resemble similar structures in the female *Mastigoproctus*. For this reason I consider the specimen to be a female.

The lungs are not well preserved, but two pairs can be seen on the left side, if one is familiar with their appearance from the study of specimens in which all three pairs are well preserved. One spiracle is also visible. The distortion of the coxal region makes the understanding of the arrangement of the coxae difficult, unless one has familiarized oneself with the picture presented by better preserved specimens. For this reason I shall omit their description here and give a description and figures of other specimens of the species further down.

Specimen In. 7884 and 7916. Although these two pieces represent the dorsal (7884) and ventral (7916) surface of the same specimen, they were unfortunately accessioned separately. The two pieces fit perfectly together, when brought in contact with each other (Figures 30, 48, 88, 222 and 224).

The carapace is missing. The dorsal surface of the abdomen is preserved complete, with the first tergite. The legs are preserved as far as the end of their femora. Approximate total length of the specimen, measured from the base of the second joint of chelicerae on piece *b* showing the ventral surface, to the end of the abdomen is 9.7 mm. Abdomen 6.4 mm. long (including first tergite), 6.0 mm. wide. Median tergal area 2.87 mm. long, 3.14 mm. wide. Ninth tergite 1.00 mm. long, 1.57 mm. wide.

The interesting features of this specimen are the cheliceral coxae, the second joint of chelicerae and the genital region with the lungs. The cheliceral coxae, as shown in Figure 30 and photographically in Figure 222, have their cavities wide open. All four foramina are plainly visible, the anterior one with the articular membrane which almost closes the left foramen. Across the cheliceral second joints a membrane is visible. Its interpretation is very difficult. I am inclined to see in it the impression of the inner wall of the carapace superimposed on the cheliceral joints which were stretched out front-wise after death. The genital region is shown in Figures 48 and 88 and photographically in Figure 224. All three pairs of lungs are perfectly preserved and even the apodemes of their muscles are visible. Three depressions A, B and C resemble those of the type and the specimen is therefore of the same sex, presumably female. There is one additional feature visible in the preserved cup-like depression of the triangular depression A; it shows the two receptacles as drawn in Figure 48, in the insert. They are in the same place as in the depression A of *Cryptomartus hindi* (q.v.), which proves that a pair of receptacles are regularly present in *Anthracomarti*.

Specimen In. 15884 is also a female. The specimen is in three pieces. Piece *a* shows the dorsal surface of the carapace and abdomen and three legs as far as the end of their femora. Pieces *b* and *c* form together the ventral surface with three pairs of legs as far as the end of their femora. The specimen is badly distorted. The carapace is compressed out of shape laterally, the tergal median area and the ninth tergite cannot be measured, but the genital area is clearly visible. Total length 8.0 mm. Carapace 3.0 mm. long, abdomen 5.0 mm.

Specimen In. 15857. Androtype. Male. Figures 87 and 211, 212). A fairly well preserved specimen consisting of two pieces. Piece *a* shows the dorsal surface of the carapace and abdomen with the first tergite fully exposed. The carapace is slightly distorted (Figure 211). Its surface is coarsely punctured. Abdominal tergite 2 + 3 and all visible joints of legs also coarsely punctured, but the rest of the abdomen appears to be evenly dull. On the left side of the piece three joints of the palp are visible, also the trochanter of the first leg, the second and third legs both complete and the femur of the fourth leg. On the right side the femur of the second leg, the complete third leg and a portion of the fourth leg as far

as the end of the patella are visible. Piece *b* shows the ventral surface. The abdomen is complete (Figure 212) but for a slight piece on each side, the anal operculum is clearly circumvallated, the three depressions A, B and C are very distinct, but of the lungs only the first and third pair are preserved and they can be seen only with difficulty. The first right leg is preserved as far as the end of the patella, both legs of the third pair appear to be complete, the fourth right leg is also complete, but cannot be measured beyond the patella because of its position. The fourth left leg is preserved only to the end of its patella. Inside the fourth right femur a median longitudinal crest separates the two parallel furrows which in life must have been occupied by the flexors of the knee. Several coxae are visible, including those of the chelicerae.

Total length 13.5 mm. Carapace 4.7 mm. long, ca. 4.3 mm. wide. Abdomen 7.4 mm. long, 6.3 mm. wide, i.e. distinctly narrower than wide (in the type it is as wide as long). Medial tergal area 4.00 mm. long, 4.29 mm. wide. Ninth tergite 1.21 mm. long, 1.71 mm. wide.

Legs	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	1.60	1.00	—	—	—	?
II	2.00	1.15	1.15	0.50	0.75	5.55
III	2.00	1.20	1.15	0.75	1.00	6.10
IV	2.30	1.25	—	—	—	?

All legs look somewhat more slender than in the type. The ratio between the length of the second leg and that of the carapace is 1.2 as against 1.3 in the type, the ratio of the third leg, 1.3 as against 1.4. The difference is not great, but remarkable, inasmuch as it shows that the legs of the female were relatively longer than those of the male. The genital region is shown in Figure 87 and may be seen also in the photograph. Depression A has a long and narrow median cleft and a transverse median furrow and has a very different appearance from the corresponding depression of the type.

Specimen In. 18336. Male (Figures 47 and 227). This specimen consisting of two pieces, is one of Pocock's paratypes of his *A. priesti*. It is badly distorted and poorly preserved and is valuable only because of the excellent preservation of the lungs and of the three abdominal depressions. The apodemes for the attachment of the pulmonary muscles are also clearly visible. The shape of the depres-

sion A is the same as in the Androtype and very different from that of the type. So is the depression B with its sharply drawn out corners. Measurements are not possible on account of distortion, but the total length of the specimen is about 11.5 mm.

Specimen In. 7915. Presumably a male, referred to this species only with reservations, because the dorsal surface is not preserved, while the ventral one is incomplete and not well preserved. However, three left lungs and the three depressions are well visible. The cheliceral coxae are pressed out of shape. Perhaps of interest is the fossilization of the cephalothoracic organs apparently in bulk, although no individual muscles or other organs can be distinguished. Total length of the specimen ca. 11 mm. Abdomen ca. 7.4 mm. long.

Specimen In. 18334, is another of Pocock's paratypes of his *A. priesti*. It consists of two pieces, both showing only the abdomen. Piece *a* shows the dorsal surface of the abdomen with the first tergite. It is 6.4 mm. long, 6.0 mm. wide. Median tergal area 3.14 mm. long, 3.30 mm. wide. Ninth tergite 1.14 mm. long, 1.57 mm. wide. Piece *b* shows the ventral surface except in the anterior region which is considerably raised above the level of the rest and shows the first and the 2 + 3 tergites.

Specimen In. 18335, another of Pocock's paratypes of his *A. priesti*, is represented by a single piece showing only the dorsal surface of the body. Total length 9.6 mm. Carapace 3.6 mm. long, 3.6 mm. wide. Abdomen 6.0 mm. long, 6.1 mm. wide. Median tergal area 2.86 mm. long, 3.14 mm. wide. Ninth tergite 1.00 mm. long, 1.57 mm. wide. If the width of the abdomen is a regular feature of the sex, then this specimen must have been a female.

Specimen In. 13956, is another of Pocock's paratypes of his *A. priesti*. Originally it consisted of two pieces. Piece *a* is at present in the same condition in which it was and shows the dorsal surface of the carapace and abdomen, with the longitudinal ventral lines superimpressed, but otherwise well preserved. Piece *b* consisted originally of two pieces which were cemented together. Noticing that some structures were disappearing from view in the crack, I dissolved the cement and separated the two pieces. Thus two complete legs became exposed, one of them with a pair of claws, and a cavity in the matrix under the anterior end of the cephalothorax. By removing the left chelicera and maxilla, a view was obtained of

the mesial surface of the right chelicera and maxilla in profile (Figure 86). The coxal spine or thorn is visible, corresponding to the posterior foramen which may be seen in other specimens in which the cheliceral coxae appear as cavities. The abdomen is complete with its first tergite. Total length of the specimen 12.0 mm. Carapace 4.0 mm. long, 4.0 mm. wide. Abdomen 6.9 mm. long, 7.3 mm. wide. Median tergal area 3.29 mm. long, 3.71 mm. wide. Ninth tergite, 1.00 mm. long, 1.57 mm. wide. On the same basis as the preceding specimen, this specimen probably was also a female.

Specimen In. 15895 consists of two pieces. Piece *a* shows the dorsal surface of the body and several femora. The carapace is pressed out of shape, but resembles more that of the Androtype, than of the type. Piece *b* shows part of the ventral surface badly broken up and with the anterior end missing. Total length 12.3 mm. Carapace approximately 5.15 mm. long, 4.8 mm. wide. Abdomen, including first tergite, 8.0 mm. long, 7.15 mm. wide (measured from left edge to middle and then doubled). Median tergal area 3.43 mm. long, 3.71 mm. wide. Ninth tergite 1.14 mm. long, 1.71 mm. wide. The first tergite is completely covered by the carapace, but plainly visible nevertheless. The surface of the carapace and of the tergite 2 + 3 is coarsely punctured. On the basis of the proportions of its abdomen, this specimen must have been a male.

Specimen In. 31251 is represented by a single piece (No. 23 of W. Egginton). It shows the ventral surface of the abdomen from the posterior end of the fourth tergite backwards, while the anterior sternites are hidden under mineral matter showing the anterior tergites. The first tergite is fully exposed. Tergite 2 + 3 shows dark brown pigmentation and evenly distributed granules, tergite 4 also shows pigmentation and some granules on the pigmented area. It is evident that in this specimen the external surface of the tergites is exposed and not their mold. The carapace is missing, its place is occupied by what seems to be the fossilized cephalothoracic internal organs without traces of their individual outlines. Total length of the specimen ca. 14 mm. Abdomen 6.4 mm. long, 6.3 mm. wide.

Cleptomartus planus n. sp.

Type and only specimen, In. 7918. Figures 90-93 and 218-220. The specimen consists of two pieces from the bed of nodular iron-

stone about 10 feet above the thick or 10 yard coal, Coseley Staffs. W. Madeley collection of the British Museum.

Piece *a* shows the dorsal surface of the carapace and abdomen, one right and one left leg (Figure 218). Piece *b* (Figure 219) shows the carapace and the anterior tergites elevated above the rest of the abdomen on which the posterior sternites are visible. On the same piece are preserved the median joints of both chelicerae, sections of both pedipalpi, one (presumably the third) left leg and the fourth right leg. At first sight the specimen greatly resembles *C. plautus*, but relative measurements of the median tergal area, of the ninth tergite and of the angle formed by the two sides of the eighth sternite make the distinction of the two species a simple matter.

Total length 9.0 mm. Carapace 3.0 mm. long, 3.0 mm. wide, flat, distinctly narrowed anteriorly, evenly rounded in front, transversely straight behind. Surface of carapace smooth. Eyes wanting. Abdomen relatively longer than in *C. plautus*. Its median length from the anterior edge of tergite 2 + 3 (the first tergite is not distinctly visible) to the posterior end of the body is 6.0 mm. Its greatest width is at the level of the marginal fields of the seventh tergite (Figure 90) where it measures 5.3 mm. It is dorsally longitudinally evenly convex, but slightly depressed in the anterior median region. The sides are also evenly convex, but form a distinct angle with the median tergal area. Length of tergite 2 + 3 in median line 1.05 mm. Median tergal area occupied by the fourth to eighth tergites is 2.9 mm. long, 2.4 mm. wide. Ninth tergite 1.25 mm. long, 1.45 mm. wide. Average length of the tergites of the median tergal area is 0.6 mm. the sixth tergite being slightly the longest, the fourth and third slightly shorter, the seventh and eighth the shortest, but even the difference between the sixth and the eighth tergites amounting to only 0.1 mm. Neither the coxae, nor the sternum are visible on either of the two pieces, and only the last three sternites are visible on piece *b* (Figure 91). The angle formed by the sides of the eighth sternite is ca. 90°, measured with the aid of a goniometric ocular. A deep angular depression in front of this angle marks the posterior end of the arched area present in other species and first described by Pocock in *C. hindi* and *C. priesti*. The purpose or function of this area is not known. The anal operculum (Figure 92) is very well preserved. It is circular and its anterior valve is larger than the posterior one, as in all species of this order of Arachnida.

The chelicerae are preserved only as far as the end of the second joint. This joint, however, is fossilized as such and is unusually well visible (Figure 93 and 220). The pair is situated in a plane at right angles to the longitudinal axis of the body. The length of the joint is only 1.1 mm., i.e. ca. 2.7 times shorter than the carapace. The two joints are parallel to each other for four fifths of their length, but then become strongly divergent. In side-view they appear to be quite straight, wherein this species differs from *C. plantus* in which they are concave in front. The third joint is not visible. Perhaps the fine, curved line running parallel to the diverging edge of the second joint, represents the edge of a portion of the third joint, but this is far from certain. The measurements of the legs are as follows: Third leg, femur 1.35, patella 0.75, tibia 0.75, metatarsus 0.45, tarsus 0.50, total 3.80 mm. Fourth leg, femur 1.50, patella 0.80, tibia 0.80, metatarsus 0.50, tarsus 0.80, total 4.40. The tarsus is distinctly longer than the metatarsus.

Genus *Cryptomartus* Petrunkevitch, 1945

Type *C. hindi* (Pocock), sub *Anthracomartus*

This genus was proposed by me for the two species described by Pocock under the generic name of *Anthracomartus*, namely *A. hindi* and *A. priesti*. At that time I had no opportunity to examine specimens belonging to either of these species and depended entirely upon Pocock's descriptions and figures. Now the situation is very different. Although it is regrettable that Pocock's types could not be sent to me for study, his paratypes were sent together with several other specimens. Fortunately the genus proved to be valid, even though its characters had to be modified and extended. At present the chief character of the genus is derived from the shape and the structure of the carapace. It is very high, with steep sides and a longitudinal median crest on its slanting cephalic portion, extending to the very edge of the carapace. Pocock did not know of the existence of this crest because his specimens were insufficiently cleared of extraneous matter which completely filled the cavity of the carapace and obstructed the view of its structure. Pocock's key for the separation of the two species was based on the difference in their size and the relative shape of the penultimate tergite (his seventh, my ninth) and of the "triangular lateral pleural plate." Since I have found that four of Pocock's paratypes of his *A. priesti* belong to a different genus and species, a new key had to be prepared for the

distinction of *C. hindi* from *C. priesti*. This key is based on characters present in the specimens which I have found to possess the crested carapace.

Key to Species of *Cryptomartus*

1. Ninth median tergal plate as long as wide or even slightly longer. Median tergal area longer than wide in ratio 1 : 0.7 to 0.8. Angle formed by the sides of the eighth sternite ca 110° to 115°. Larger species. Mature individuals up to 25 mm. long. *C. hindi*.
- Ratio of length to width of ninth tergal plate 1 : 1.4 to 1.6. Median tergal area only slightly longer than wide in ratio 1 : 0.9. Angle formed by the sides of the eighth sternite ca 145°. Smaller species. Mature individuals from 9.5 to 13.5 mm. long. *C. priesti*.

Cryptomartus hindi (Pocock)

Anthracomartus hindi Pocock, Terrestrial Carboniferous Arachnida, 1911, pp. 64 to 67. Figures 30-32 and Figure 3 on Plate III.

Cryptomartus hindi Petrunkevitch, Palaeozoic Arachnida of Illinois, 1945, p. 49.

According to Pocock's own statement "The type of this species is a cast (No. 12148), in the Geological Survey Museum, of the underside of the dorsal surface of a specimen from Dudley belonging to Dr. Kidston." In addition to the type, he described seven other specimens, all from the Upper Carboniferous of Coseley, Staffs. Seven specimens were sent to me for study, three of which are Pocock's paratypes. They are numbered (4), (5) and (6) on page 66 of his Monograph. One specimen is labelled as one of Pocock's paratypes of his *A. priesti*, but I can find no reference to it in Pocock's paper. One specimen (18583) is from a different horizon.

The total length of Pocock's specimens, as stated by him, varies from 25 mm. in the type, to 13 mm. in the specimen listed by him as No. (7). The total length of the smallest specimen before me, which is not one of Pocock's paratypes, but which I believe to belong to this species is 14.5 mm. (In. 18338), with the abdomen 8.1 mm. long, and 7.7 mm. wide. Specimen In. 18337 (which is labelled as Pocock's paratype of *A. priesti* but which belongs to the species *hindi*), is also 14.5 mm. long: its abdomen is 9 mm. long and 7.5 mm. wide.

Thus measurements of all specimens in which both the length and the width of the abdomen could be determined with certainty, show definitely that the abdomen of *C. hindi* is slightly longer than wide, narrowed in front to the width of the carapace, evenly rounded behind. In his restoration of a complete specimen as it would appear in life in side-view (Pocock's figure 32 on page 66) Pocock represents the ventral surface of the abdomen as considerably more convex than the dorsal surface. This is not so. For some reason in all specimens of *Anthracomarti* which I have studied (and this includes American species as well as European ones), the dorsal surface of the abdomen invariably appears to be convex, instead of concave, as it should be, and yet is a mold and not a cast. This can mean only one thing, namely that the dorsal wall was pressed into the interior of the abdomen as far as it could go. I have already discussed this phenomenon above and suggested that the reason for it must be sought in the presence of soft membranes between the dorsal abdominal plates. The measure of inversion is, of course, also the measure of the normal convexity of the abdomen in life. In Figure 66 I have drawn outlines of plastic clay casts cut across, to show the shape of the carapace and abdomen of the two species of *Cryptomartus* and the two species of *Cleptomartus*. From these sections it is evident that the dorsal surface of *C. hindi* was much more convex than the ventral one, Pocock's "suggested restoration of the ventral surface" shown in his Figure 31 is wrong in several respects. The coxae are too far apart and the cheliceral coxae are not shown. The two converging lines delimiting the arched area are too long, since in the specimens they reach only to the eighth sternite. The appearance of the genital region is also not as it is in specimen In. 13955 which is Pocock's paratype No. (4) and which will be discussed further down. Nor does Pocock's Figure 30 show the crest.

Specimen In. 13955. Pocock's paratype No. (4). This beautiful specimen consisting of two pieces, is shown photographically in Figures 195 to 198 and in drawings in Figures 64 and 65 and 67. The outline of the crest is shown in Figure 67, but it appears quite clearly also in the photograph (Figure 197). Like the carapace itself, the crest appears, of course, as a groove and not as an elevation. The surface of both the carapace and the crest is coarsely punctate and was therefore granular in life. The coxal region is fairly well visible, though not as sharply as in some other specimens of *Anthra-*

comarti. It is shown in Figure 65. The cheliceral coxae in that figure are introduced from another specimen (18338) and are represented with the four foramina, although the latter are not visible in either specimen of *C. hindi*. The three abdominal depressions A, B and C are shown in Figure 71. In the depression A not only the two receptacles, but also the transversely elongated genital opening are so well preserved that they came out even in the photograph (Figure 198). From the appearance of this depression and the presence of two receptacles I conclude that this specimen is a mature female. At each side of the rather inconspicuous depression C a spiracle is visible, but of the book-lungs only the first pair can be recognized on the second sternite, and even that not very distinctly. Although Pocock gives the total length of this specimen as 21.5 mm. and the length of its abdomen as 15.5 mm., my measurements after cleaning and exposure of all parts are as follows: Total length ca. 23 mm. Carapace 8.0 mm. wide, its length not exactly measurable because of a transverse fold. Abdomen 16.56 mm. long, 13.7 mm. wide in middle, only 8.0 mm. wide in front. Median tergal area 8.3 mm. long, 5.7 mm. wide. Ninth (penultimate) tergite 2.86 mm. long, 3.10 mm. wide.

The arched area of the abdomen occupies only three sternites, the fifth, sixth and seventh, and in the latter a median triangular depression divides it into a right and left half. The angle formed by the sides of the eighth sternite cannot be measured because of a lateral constriction of the abdominal wall, but it seems to be only a trifle over 90°. The entire surface of the abdomen on both sides is coarsely punctured. Of the appendages only the femora are preserved. The first tergite is fully exposed to view. Coseley, Staffs.

Specimen No. 31250, Pocock's paratype No. (5) (No. 22 of the Egginton collection). Two pieces. Only carapace and abdomen preserved and the carapace so poorly, that the crest is not visible and the species is identifiable only by its size and structure of the abdomen. Total length 22 mm. Carapace 7.14 long, 7.71 wide, but the measurement of the length is evidently smaller than it should be, owing to poor preservation and incompleteness of outline. Abdomen 15.7 mm. long (with the first tergite which is visible, but not well preserved. Without it the abdomen is 15.0 mm. long), 13.14 mm. wide in middle, 7.71 mm. wide in front. Median tergal area 7.71 mm. long, 5.71 mm. wide. Ninth tergite 3.00 mm. long, 3.30 mm. wide.

Angle formed by the sides of the eighth sternite ca. 85° . Coseley, Staffs.

Specimen In. 31253, Pocock's paratype No. (6), (No. 29 of the Egginton collection). Two pieces, both showing only the dorsal surface of the abdomen with the first tergite complete. Abdomen 15 mm. long, 14 mm. wide. Median tergal area 7.4 mm. long, 5.7 mm. wide. Ninth tergite 3.14 mm. long, 3.14 mm. wide. Coseley, Staffs.

Specimen In. 18337, labelled as one of Pocock's paratypes of *A. priesti*, is possibly his No. (7) on p. 66, presented to the British Museum by S. Priest, Esq., April 1916. Two pieces. Piece *a* showing the dorsal surface of carapace and abdomen, piece *b* the ventral surface. No appendages preserved. First tergite visible, but not sharply delimited. Total length 14.5 mm. Abdomen 9.0 mm. long, 7.5 mm. wide. Median tergal area 4.14 mm. long, 3.29 mm. wide. Ninth tergite 2.14 mm. long, 2.14 mm. wide. Crest visible, but poorly preserved. Coseley, Staffs.

Specimen In. 18338. Two pieces. Piece *a* shows the dorsal surface of the carapace and abdomen, without any appendages. The crest is very sharply outlined. The first tergite is visible. The median tergal area is distorted. Piece *b* shows the ventral surface including also the first leg complete, the second left leg to the end of the femur, the right first leg to the end of the tibia and the right second leg also to the end of the tibia. The cheliceral and pedipalpal coxae are recognizable, but not well preserved. Total length 14.5 mm. Carapace 5.0 mm. long, 4.8 mm. wide. Abdomen, including the first tergite, 8.7 mm. long, 8.3 mm. wide (measured to middle on the right side of the specimen and the measurement doubled). Median tergal area cannot be measured on account of distortion. Ninth tergite 2.14 mm. long, 2.14 mm. wide. Angle formed by the sides of the eighth sternite ca. 90° . The first leg is shown in Figure 69, its claw in Figure 70. The preservation of the leg is so unusually good that it was even possible to photograph the claw (Figure 199). It is at the end of a very well developed onychium, which is undoubtedly one of the reasons why the claws of *Anthracomarti* are so rarely preserved. Above the claw the ends of six pointed bristles are visible, but there seems to be neither a lower single claw, nor any tenent hairs present. The measurements of the first leg are as follows: femur 3.2, patella 1.2, tibia 1.6, metatarsus 0.8, tarsus 1.1;

total 7.9 mm. It is a young specimen with a still undeveloped genital region. Coseley, Staffs. Presented to the British Museum by Mr. S. Priest, April 1916.

Specimen In. 13910. Two pieces. Piece *a* shows the dorsal surface of the abdomen without the first tergite which is missing. Piece *b* shows the ventral surface of the abdomen. Carapace and appendages missing on both pieces. The specimen is undoubtedly a very young one. Its anal operculum is very well preserved and for this reason is shown in Figure 68. Perhaps an interesting point of its structure is the eccentric thickening of the wall around it. Abdomen, without the first tergite, 9.3 mm. long, 8.6 mm. wide. Median tergal area 4.1 mm. long, 3.7 mm. wide. Ninth tergite 2.0 mm. long, 2.0 mm. wide. Angle formed by the sides of the eighth sternite ca. 90°. Judging by the size of the abdomen, the specimen must have been about 15 mm. long. Coseley, Staffs.

Specimen In. 18583 is of particular interest because it comes from an older formation than the other specimens, namely from the Middle Coal Measures of Sparth Bottoms. It was presented to the British Museum by W. H. Sutcliffe in 1906. The specimen consists of two pieces, both showing only the dorsal surface of the abdomen, and that badly distorted. The carapace is missing. From the general appearance of the abdomen and measurements, as far as they are possible, I am unable to detect any difference between this specimen and the other six specimens of *C. hindi*. Abdomen without the first tergite 17 mm. long, 16 mm. wide. Median tergal area 7.4 mm. long, 5.2 mm. wide. Ninth tergite 3.6 mm. long, 3.6 mm. wide. Judging by the size of the abdomen, the specimen was about 25 mm. long in life, possibly 26 mm., but at any rate not appreciably larger than Pocock's type.

Cryptomartus priesti (Pocock)

Anthracomartus priesti Pocock, Terrestrial Carboniferous Arachnida, 1911, pp. 67-68. Figures 33-34.

Cryptomartus priesti Petrunkevitch, Pal. Arach. Illinois, 1945, p. 49.

Pocock's restoration of this species suffers from the same defects as his restoration of the preceding species. Moreover, he omitted to give a picture of his type, his figures 33 and 34 being based on a study of several specimens. Fortunately he says in his key to

species on page 63 that the ninth tergite (he calls it the seventh) is much shorter than wide. I say "fortunately," because this character used in combination with the figure made it possible to sort out the specimens which show these characters. I was unable to examine the type on account of the rules of the British Museum. Of Pocock's seven paratypes sent to me for study, four proved to belong to *C. plantus* (q.v.), and one to *C. hindi*. Two paratypes conformed with the above character and figures as far as the latter go. At present, then, I regard as belonging to the same species with Pocock's type of *Cryptomartus priesti* the following six specimens: In. 22842 (Pocock's paratype No. (3)), In. 31237 (Pocock's paratype No. (5)), In. 7893, In. 3126, In. 15858 and In. 31268. All these specimens are from the same horizon and the same locality, the Upper Carboniferous Coal Measures of Coseley, Staffs. Three of them are males, two are females and one is presumably an exuvium.

Specimen In. 22842 (Pocock's paratype No. (3). Figures 75, 80 and 213. Two pieces. Piece *a* shows the dorsal surface of the carapace and abdomen, pieces of both palpi, first femur and three complete legs on the left side and three femora on the right side. The carapace is well preserved, with the crest sharply outlined. The abdomen badly distorted. All parts coarsely punctured. Piece *b* shows the ventral surface with the same appendages. The cheliceral coxae are narrow and long, with the four foramina clearly visible. The abdomen is incomplete and poorly preserved, but the genital region is clear. It is shown photographically in Figure 213. The three right book-lungs are well preserved. The specimen is a mature male. Total length 10.0 mm. Carapace 4.1 mm. long, 3.3 mm. wide (Pocock gives the length as 4.5, the width as 3.5. I think he measured the carapace to the anterior edge of the tergite which he calls the first and which is tergite 2 + 3 in my interpretation. The specimen is distended. I think my measurement is the correct one). Abdomen 5.8 mm. long, 5.1 mm. wide (measured to middle and the measurement doubled). Tergal median area 2.7 mm. long, 2.4 mm. wide. Ninth tergite cannot be measured.

Legs	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	1.71	—	—	—	—	?
II	1.71	1.00	1.00	0.57	1.00	5.28
III	1.86	1.00	1.00	0.57	1.00	5.43
IV	2.00	1.00	1.00	0.57	1.00	5.57

The tarsus is longer than the metatarsus in all three legs. At the end of the fourth leg (Figure 75) a pair of claws may be seen, but in this position the onychium, if it was present, cannot be seen.

Specimen In. 31237 (Pocock's paratype No. 5). Figures 29, 72, 208 and 215. This specimen is also a mature male. It is represented by two pieces. Piece *a* shows the dorsal surface of the body and three pairs of legs as far as the end of the femora. The carapace is well preserved, with the crest sharply outlined. The abdomen is badly distorted. Piece *b* shows the ventral surface with the abdomen also badly distorted, but the genital region is well preserved and shows the characteristic shape of depression A, found in males (Figure 72 and photograph 215). Of interest is the excellent preservation of the cheliceral coxae, shown in Figure 29 and photograph 208. It will be noticed that the cheliceral coxae are quite narrow, with parallel sides, each with the characteristic two foramina, the anterior one leading into the second joint, the posterior into a ventral spine. In front of the coxae the second joint of both chelicerae are visible, but are displaced to the right. The pedipalpal coxae are also narrow and long, with parallel sides. These four coxae appear as deep depressions with vertical walls. The foramina of the cheliceral coxae are at the bottom of the depression. The pedipalpal coxae show a row of round, coarse punctures, evidently corresponding to a row of external tubercles. Only the right coxa is shown in the figure. Total length of specimen 13.0 mm. Other measurements are impossible on account of distortion and poor preservation.

Specimen In. 7893—Figures 74, 77-79, 201, 203, 210, 225. This specimen is in many respects of considerable interest. Piece *a* shows the dorsal surface of the body and two legs on the left side and four legs on the right side of the nodule. The carapace is in perfect condition, showing the crest sharply outlined and like the rest of the carapace coarsely punctured (Figure 77). To show the crest as it must have looked in a living specimen, I made a cast of plastic clay and reproduced the latter photographically in Figure 201. The abdomen is also excellently preserved as may be judged by its photograph in Figure 203. The first tergite is fully exposed. The segmentation of the abdomen is indicated in Figure 74. Three of the legs are preserved to the end of the tarsus, showing that the latter is longer than the metatarsus. Piece *b* shows the ventral surface and the second joints of chelicerae. The latter are situated in a plane

at right angles to the axis of the body, one of the reasons, why they are usually not visible, unless the matrix surrounding them is removed to a considerable depth, as I did in this case. This joint of the chelicerae is shown from in front in Figure 78 and photographically in Figure 225. The outer edges of this pair of joints are parallel but the inner ones are strongly divergent. In profile (Figure 79) the joints are strongly concave in front. Their length and shape make me think that this specimen is also a male, although the genital region is filled with smooth matrix, showing no depressions, nor any segmentation. But the "arched area" of the abdomen is very well preserved and is reproduced photographically in Figure 210. Total length 13.5 mm. Carapace 5.7 mm. long, 4.6 mm. wide. Abdomen 7.3 mm. long with the first tergite, 6.6 mm. wide. Median tergal area 3.86 mm. long, 3.71 mm. wide. Ninth tergite 1.14 mm. long, 1.57 mm. wide. Chelicer second joint 1.4 mm. long, i.e. fully one quarter as long as the carapace. The angle formed by the sides of the eighth sternite is ca. 115° .

Specimen In. 31264—Figures 41, 204 and 205. This specimen is also marked as No. 48 of the W. Egginton Collection of the British Museum. It is of special interest for two reasons. First, because the carapace is severed from the abdomen. This is probably due to its being an exuvium, although it is also possible that the specimen decayed and was disrupted before it was fossilized. Whichever the correct interpretation may be, the result is the same, namely that the abdomen is completely exposed, with the anterior edge of the first tergite clearly visible and showing its thickening for the attachment of the connecting membrane. The length of the abdomen in the median line is 6.4 mm., the width 6.4 mm. This gives the approximate total length of the specimen in life as ca. 10 mm. Median tergal area 3.29 mm. long, 3.29 mm. wide. Ninth tergite 1.14 mm. long, 1.71 mm. wide. Angle formed by the sides of the eighth sternite 115° .

The second reason why this specimen is interesting lies in the preservation of piece *b*. Originally this piece showed the same (dorsal) surface of the abdomen. Something in its appearance made me think that deeper down the ventral body-wall must be still in existence, overlaid and concealed from view by mineral deposit filling out the abdominal cavity. Proceeding on that assumption I exposed the ventral surface of the abdomen posteriorly and

laterally, but left the anterior tergal plates intact. The result is shown photographically in Figure 205.

Specimen In. 31268—Figures 35, 53, 54, 76, 206, 207, 209 and 214. (This specimen is marked also No. 53 of the W. Egginton Collection in the British Museum.) This specimen is of the greatest importance for the understanding of the arrangement of the coxae and of the segmentation of the abdomen. It is unusually well preserved and three legs are complete, so that of the four pairs only the last cannot be measured, both legs being preserved only as far as the end of the femur. Piece *a* showing the dorsal surface is reproduced photographically in Figure 211, Piece *b* showing the ventral surface in Figure 212. The segmentation of the abdomen is shown in Figures 53 and 54, and the two surfaces superimposed in two colors in Figure 35. Figure 76 shows the ventral aspect of the specimen with missing appendages restored and represented in dotted lines. For some reason unknown to me, this specimen does not show the "arched area" and the latter is therefore omitted from the drawing. The genital region is shown photographically in Figure 214. It is extremely well preserved, although slightly pressed out of shape. Depression A leaves no doubt that it is a female. At the sides of the depressions the three pairs of lungs are completely and beautifully preserved together with their spiracles and the apodemes for the pulmonary muscles. No less beautifully preserved are the coxae, including all six pairs. The cheliceral coxae (Figure 209) happen to be rather widely open, showing the four foramina to their advantage. The outer walls of the cheliceral coxae partly obstruct the view of the pedipalpal coxae, which appear therefore as narrow slits. The wide mouth may be seen behind these four coxae, and behind the mouth a smooth trough leading to the end of the cephalothorax. The trough is either the foregut itself, or else the endosternite underlying it. Total length 10.14 mm. Carapace 4.29 mm. long, 4.00 mm. wide. Abdomen without the first tergite which is not visible, 5.86 mm. long, 5.71 mm. wide, measured to middle and the measurement doubled. Median tergal area 2.86 mm. long, 2.86 mm. wide. Ninth tergite 1.00 mm. long, 1.43 mm. wide. Angle formed by the sides of the eighth sternite ca. 120°.

The legs are amazingly alike and only 1.2 times as long as the carapace, except the fourth leg, which must have been longer if judged by its femur.

Legs	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	1.57	1.00	1.00	0.57	1.00	5.14
II	1.57	1.00	1.00	0.57	1.00	5.14
III	1.57	1.00	1.00	0.57	1.00	5.14
IV	2.14	—	—	—	—	—

Specimen In. 15858—Figures 73, 200 and 202. This specimen is also very well preserved. Its first leg is complete, the others preserved to the end of the patella. Consequently it was possible to make a good cast of plastic clay and to photograph it in three-quarter view (Figure 202) to show the shape of the body and the general appearance of the animal. The crest is shown also photographically in Figure 200 and a drawing of the genital area is given in Figure 73. The specimen is a female of approximately 12 mm. length. Carapace 4.57 mm. long, 4.00 mm. wide. Abdomen, including the first tergite which is plainly visible, 7.14 mm. long, 6.00 mm. wide. Median tergal area 3.57 mm. long, 3.14 mm. wide. Ninth tergite 1.00 mm. long, 1.57 mm. wide. Angle formed by the sides of the eighth sternite ca. 120°. First leg, femur 1.86, patella 1.00, tibia 1.00, metatarsus 0.57, tarsus 0.86. Total 5.29 mm. Second and third femur 1.86 mm. Fourth femur 2.14 mm.

Genus *Coryphomartus* Petrunkevitch, 1945

Type *C. triangularis* (Petrunkevitch), sub *Anthracomartus*

The type of this genus, represented by a single specimen from the Upper Coal Measures of Joggins Mines, Nova Scotia, was described by me in 1913. The confusion of lines made me give a wrong interpretation of the dorsal surface. This time I was able to study the specimen once more, to clean it and to give new, correct figures. The genus is represented by a single species. The characters of the genus are given in the key. The specimen is shown photographically, as it appears now, in Figure 191. Figure 59 shows the carapace and the abdomen with the lines corrected and the segments numbered in conformity with the other specimens of *Anthracomarti*. The median tergal area formed by tergites 4 to 8 is 2.66 mm. long, 2.57 mm. wide.

Genus *Brachypyge* Woodward, 1878

Type *B. carbonis* Woodward

The characters of the genus are given in the key. The segmentation of the abdomen is shown in Figures 60 and 61, based on the original

drawing in Woodward's paper, and conforms with the other species of *Anthracomarti*. For the original description of the specimen, the reader is referred to Woodward, H., *Geol. Magazine*, (2), Vol. V, 1878, pp. 433-436, Plate XI. For a photograph of the type see P. Pruvost, *Mem. Mus. R. Hist. Nat. de Belgique*, No. 44, 1930. Plate XI, figures 1 and 2. Additional data concerning the species on pp. 210 - 212.

Genus *Maiocercus* Pocock, 1911

Type *M. carbonis* (Howard and Thomas), sub *Eophrynus*.

The characters of this genus are given in the key. As long as the genus is recognized, the type species is, of course, "*carbonis*" and not *celticus* as given in my Monograph of 1913. Pocock had to find a new name, because in 1902 he referred this species to Woodward's genus *Brachypyge*, the type of which is a species which happens also to have the name *carbonis*. Pocock retained the name *celticus* in 1911 possibly out of oversight. Pruvost recognized the genus *Maiocercus* in 1911 when he referred to it what he thought to be a new species, *Maiocercus orbicularis* Gill. Of this species Pruvost gave excellent photographs of two French specimens on Plate XXIII and a detailed description with two line-drawings (pages 359-363). In 1930 Pruvost dropped the Genus *Maiocercus*, synonymizing it with *Brachypyge* and the species *M. carbonis* Pruvost (nec Gill) with *B. celtica* Pocock (p. 213). He gave a photograph of a Belgian specimen on Plate XI. I have explained above the reasons why I retain the Genus *Maiocercus* here. In Figures 62 and 63 I have reproduced Pruvost's figures of 1919, but with the introduction of segmentation conforming with the one adopted in the present paper.

Evolutionary trends in *Anthracomarti*

The ideas concerning evolutionary trends in *Anthracomarti*, which I put forward in 1945 have to be considerably modified by the discovery that the Order as universally recognized at that time, contained definitely unrelated genera. Now that the Order *Anthracomarti* is restricted here to the seven closely related genera, the obvious fact emerges that all seven have the same fixed number of abdominal segments. They also have the same number of book-lungs and the same number and type of structures in the genital region, at least in so far as four species of two genera may be adduced in evidence. That leaves only modifications of the carapace, which I have used for the

separation of genera. Of course, the chief character of the new Subclass Stethostomata which I proposed for the inclusion of Anthracomarti and Haptopoda, is in itself evidence of an important trend which reached its climax in these two Orders. Perhaps the fact of their extinction was due to the inability of the abdomen to undergo any change involving segmentation, and to the impossibility of returning to a less specialized arrangement of the coxal region.

III. SUBCLASS SOLUTA

Introductory Remarks.

This Subclass, as its name implies, is proposed here for the inclusion of a single Order Trigonotarbi, in which certain characters were still in a labile condition when its representatives faced extinction. The chief of these characters was the manner of juncture between the cephalothorax and the abdomen and the consequent fate of the first abdominal segment. We have seen that in Latigastra there is a trend to lose the first segment. Sometimes the entire segment disappears, at other times the sternite is normal, but the tergite is either shortened or fused with the carapace. In Caulogastra the reduction of the first segment is accomplished through peripheral constriction, and not by total shortening. It reaches its climax in Araneae where it is reduced to a very slender pedicel. Now in Trigonotarbi the behavior of the first segment and the manner of juncture between the abdomen and the cephalothorax differs in different genera. In *Trigonotarbus* the juncture occupies the full width of the abdomen and the first tergite is somewhat abbreviated. In *Anthracosiro* the juncture is also full width, but there is a distinct, though not considerable constriction between the carapace and the abdomen, and the first tergite is represented only by the soft connecting membrane with its dorsal muscle fibers. In *Pleophrynus* the first tergite is as wide as the carapace, but it is connected with the latter only by its middle third. *Eophrynus* has probably the same type of connection, while in *Palaeocharinus*, judging by Hirst's Figure 4, the connection most resembles that described by me in the present paper for species of Anthracomarti.

The second important character is furnished by the segmentation of the abdomen. Here a distinct trend may be observed toward a loss of posterior segments. *Palaeocharinus*, according to Hirst, has an abdomen composed of eleven segments the last two of which are reduced to little, short cylinders or rings forming a pygidium.

Anthracosiro, as we shall see, has ten abdominal segments, *Eophrynus* and allied genera have nine segments, *Trigonotarbus* has eight segments. *Trigonomartus*, with related genera, has also only eight segments, but there is a difference in the structure of the last segment in *Trigonomartidae* as compared with that in all other *Trigonotarbi*. In *Trigonomartidae* the last tergite has a pair of marginal fields or plates, in the other genera it has none. Instead, the single plate of which it is composed is bordered in front by the median plate of the penultimate tergite and on the sides by the marginal plates of the penultimate segment, an arrangement made possible by the great curvature of the tergite. In these genera the last tergite is also bent under in the same sense as in the *Anthracomarti*, appearing on the ventral side of the abdomen. Here the sternites have no marginal plates, but the penultimate sternite is bent almost as a hairpin, enclosing in the space between its two arms the last sternite with the anal operculum and the ventral portion of the last tergite. A distinct line separates the tergite from the sternite in *Eophrynus* and *Pleophrynus*. In *Anthracosiro* the line is faint, but visible. I have indicated it in Figure 114 by a broken line. In *Trigonotarbus* (Figure 111) it is very faint in three specimens and not visible in the others, this being the reason why Pocock overlooked it. On the other hand in *Trigonomartidae* the last tergite does not extend unto the ventral surface. The last sternite is biconvex and occupies the entire end of the ventral surface of the abdomen.

8. Order TRIGONOTARBI, new Characters of the Order

Fossil Arachnida in which the abdomen is joined to the cephalothorax either by the full width of the carapace or only by a median portion of it, while the width of the first tergite remains the same as that of the carapace. Carapace entire, of various shapes, often with a pair of eyes. Abdomen composed of from eleven to eight segments, not counting the anal operculum. The latter is situated on the last sternite and has an anterior and a posterior valve. The tergites are divided into three longitudinal rows, so that each tergite has a single, median, and a pair of lateral, marginal, plates. The last tergite either is subdivided like the other tergites or has no marginal plates, is surrounded by the penultimate tergite and extends to the ventral surface, where it is wedged in, together with the last sternite, between the arms of the penultimate sternite. All

sternites are entire, connected with the tergites at the sides of the abdomen by a soft, pleural membrane. The arrangement of the coxae, sternum and lip are as in Araneae, all coxae more or less movable. Chelicerae two-jointed, retrovert. Pedipalpi, six-jointed, pediform. Legs seven-jointed. Tarsi with a pair of claws. Respiration by means of one to four pairs of book-lungs. Earliest known records from the Devonian of Europe, latest from the Upper Carboniferous of Europe and Pennsylvanian of North America.

The classification and the key published by me in 1945 cannot be used any more. They were based on characters derived from the study of limited material and from information contained in published descriptions given by older writers. Two families, *Pleomartidae* and *Aphantomartidae*, cannot be retained on the strength of the characters used then. They are omitted now and the genera assigned to other families. Pocock's Family *Anthracosironidae* is given recognition here and two new families are proposed, *Trigonotarbiidae* and *Trigonomartidae*.

Key to Families of Trigonotarbi

1. Abdomen composed of eleven segments, the last two of which form a small pygidium. Devonian. Family *Palaeocharinidae*.
- Abdomen composed of less than eleven segments. The last two segments never reduced to form a pygidium 2
2. Last tergite with marginal fields. Family *Trigonomartidae*, new.
- Last tergite without marginal fields, bordered on the sides by the marginal fields of the penultimate tergite and sometimes fused with the median plate of the latter 3
3. Abdomen composed of ten segments. A distinct constriction between the abdomen and the carapace, the latter with more or less parallel sides and rounded front. First tergite reduced to the connecting membrane and dorsal muscle-fibers. Last tergite fused with the median plate of the penultimate one (Figure 113). Family *Anthracosironidae*.
- Abdomen of less than ten segments. Carapace distinctly triangular 4
4. Abdomen composed of nine segments. Family *Eophrynidae*.
4. Abdomen composed of eight segments. Family *Trigonotarbiidae*.

1. Family PALAEOCHARINIDAE Hirst

Not being familiar at first hand with any representatives of this family, I refer the interested reader to Hirst's paper published in 1923 in the twelfth volume of the Annals and Magazine of Natural History. Figure 118 is a copy of Hirst's Plate XII and shows the structure of the carapace which resembles that of *Cryptomartus*, described above, and the ventral surface of an almost complete specimen of *Palaeocharinoides hornei*. The following characters are given by Hirst for the separation of his two genera:

- a. Sternum bluntly pointed posteriorly (Figure 119). Genus *Palaeocharinoides* Hirst.
- b. Sternum truncated posteriorly (Figure 120). Genus *Palaeocharinus* Hirst.

Genus *Palaeocharinoides* Hirst, 1923Type *P. hornei* Hirst

The genus is represented by a single species based on a single specimen in the collection of the British Museum.

Genus *Palaeocharinus* Hirst, 1923Type *P. rhyniensis* Hirst

Hirst did not mention which of his species he considered to represent the type of the genus. I have selected *P. rhyniensis* in conformity with the recommendation of the published Rules of Nomenclature, because this species is the best described and figured and its name is derived from the formation in which the fossil was found and which is mentioned in the title of Hirst's article. Hirst described four species of *Palaeocharinus*, all from the Rhynie Chert Bed of Aberdeenshire, *P. scourfieldi*, *P. rhyniensis*, *P. calmani* and *P. kidstoni*. He gave figures, but no key. Besides the named species, Hirst mentioned twelve other specimens to which he assigned no specific names, but which he placed in the same genus. Most of these specimens are figured and some show interesting details of structure.

2. Family ANTHRACOSIRONIDAE Pocock

Pocock proposed this family in 1903 for the inclusion of two genera, *Anthracosiro* and *Trigonotarbus*. His characters of the family were, therefore, so chosen as to apply to both genera. In the classification adopted here the two genera are separated into two families on the basis of characters which are given in the key and which I consider

to be much more important than those selected by Pocock. Moreover, the characters which I use here were not known to Pocock. He overlooked the presence of the first tergite, and did not realize that the last visible tergal plate is composed of two fused tergites. The structure of the ventral surface of *Anthracosiro* was also unknown to him. I have examined Pocock's paratype of *A. woodwardi* No. 1554, cleaned it of extraneous matter and compared it with another specimen which Pocock apparently did not see. In the light of this new evidence and with the restriction of the family to the single genus, until new material is discovered, the characters of the Family *Anthracosironidae* may be given as follows:

Body slightly, but distinctly constricted between the cephalothorax and abdomen, but the juncture definitely of the broad type. Carapace wide and flat. Abdomen composed of ten segments. All ten sternites present, but the first tergite reduced to the connecting membrane and dorsal muscle fibers (Figures 40 and 247), while the tenth is fused with the median plate of the ninth. A single pair of lungs, on the second sternite.

Pocock described two species, *A. woodwardi* and *A. fritschi*. A third species, *A. corsini*, was described by Pruvost (114-bis) in 1926 and a fourth species, *A. elongatus*, was described by Waterlot (139) in 1934. On what evidence Waterlot places his fossil from Lorraine in the Genus *Anthracosiro*, is not clear to me. The carapace is missing and the abdomen is neither complete, nor well preserved. Pruvost's *A. corsini* has a specimen from Noeux, France, for type. Later he identified another specimen from Westphalien Coal-measures of the Rhein (Kukuk—(67)—p. 441) as belonging to this species.

Genus *Anthracosiro* Pocock, 1903

Type *A. woodwardi* Pocock

Unless Pocock's paratype No. 1554 of *A. woodwardi*, which is described by me below, does not belong to the same species with the type, it is difficult to understand why it does not agree with the generic characters given by Pocock; possibly the type specimen itself was not sufficiently cleaned and its structures not sufficiently exposed and consequently not correctly described. This involves both the carapace and the abdomen. When I first examined Pocock's paratype, I found it, indeed, very inadequately cleaned of mineral matter which filled the cavities and obstructed the view of structural parts of the arachnid. In that condition it appeared to agree more or

less with Pocock's description. But after it was subjected to thorough cleaning, serious discrepancies between his description and the picture now presented by the specimen appeared. Because I saw the specimen in its original condition I still believe that Pocock's paratype No. 1554 belongs to the same species with the type and that the latter will conform with the characters of the paratype as described below when and if it should be properly cleaned. For this reason I prefer meanwhile not to give a definition of the genus, but consider it as possessing the characters of the family. This attitude is the more justified by the fact that no other genus is known to belong to the family *Anthracosironidae*.

The following key for the distinction of Pocock's species was given by him on page 407 in the tenth volume of the Geological Magazine for 1903 and is reproduced here.

- a. Terga of opisthosoma not granular throughout; the first large, more than half the length of the second, which has its anterior border mesially emarginate; joints between the proximal extremity of the lateral laminae and the median area of the eighth tergal plate not apparent. Length from 17 to 21 mm. *woodwardi*, Poc.
- b. Terga of opisthosoma finely and closely granular; the first very short, much less than half the length of the second, of which the anterior border is straight from side to side; joints between the laminae and the median area of the terga of the eighth segment present. Length about 6.5 mm. *fritschi* Pocock.

Anthracosiro woodwardi Pocock

Figures 40, 112-117, 243-248

A. woodwardi Pocock, Geol. Mag. (4), 1903, Vol. X, pp. 246-250, 405-408.

A. latipes Gill, Trans. Nat. Hist. Soc. Northumb. Durham, 1909, Vol. III, pp. 510-522. Plate XIII.

A. woodwardi Pocock, Terrestrial Carboniferous Arachnida, 1911, pp. 70-72, Figures 35, 36.

A. woodwardi Moysey, Geol. Mag., 1911, Vol. VIII, pp. 497-507, Figures 6, 9, 10.

A. woodwardi Gill, Geol. Mag., 1924, Vol. LXI, pp. 462-463, Figure 3.

Pocock described three specimens, the type No. 1551, and the paratypes No. 1553 and No. 1554, all from Coseley, Staffs. Upper Coal Measures, and a fourth specimen in W. A. Parker's collection from Sparth, near Rockdale, Middle Coal Measures.

Gill described one specimen from Crawcrook, from the Tyne coal-field near Newcastle, as the type of his species *A. latipes* which was later synonymized by Pocock with *A. woodwardi*. That specimen is in the Hancock Museum at Newcastle. Later, in 1924, Gill figured another specimen and mentioned two more specimens in the collection of Mr. Eltringham. These specimens are also from Crawcrook.

Moysey described three specimens from the coal-fields of Nottinghamshire and Derbyshire.

The specimens to be described here and belonging to the British Museum are in addition to Pocock's paratype No. 1554, numbered as follows: In. 1552 of the Johnson Collection purchased in Oct. 1886, from Coseley; In. 39769, from Middle Coal Measures at Crawcrook, collected and presented by Wm. Eltringham in July 1940.

Description of Specimen In. 1554—Two pieces, from the Upper Coal Measures of Coseley, Staffs. Figures 113 to 115, 245-246, 248. Piece *a* shows the dorsal surface of the body and portions of several appendages. Total length 14.95 mm. The carapace is somewhat distorted, but certainly rather conspicuously flat when compared with such Arachnida as *Trigonotarbus* and *Trigonomartus*. It is 4.1 mm. long, 6.5 mm. wide in middle, 5.0 mm. wide behind. Abdomen 10.85 mm. long, 6.85 mm. wide a third from posterior end. The anterior end of the carapace (Figure 245) is distinctly rounded and not produced as a small triangle in the manner shown in Pocock's figure. What appears at first sight as a little, triangular projection, proves on closer examination after wetting with alcohol to be a piece of a segment of the pedipalp. The posterior edge of the carapace gives the impression of being straight, but it is in reality slightly concave on the sides and just slightly convex in the middle. The surface of the carapace is coarsely punctate and must have been granular in life. The membrane connecting the abdomen to the carapace is visible only on the right side of the specimen. The two longitudinal lines separating the lateral fields from the median plate of the ninth tergite are not as clear as they are shown in Figure 113. Their anterior half appears as a fine, faint ridge. Beyond the constriction they become clearer outlined by a row of black punctures. No line at all can be seen, separating the tenth from the median plate of the ninth tergite. The

tenth tergite continues on the ventral surface between the two arms of the ninth sternite, but the line separating it from the tenth sternite is very faint and would be scarcely noticeable if one has not seen the corresponding line in *Pleophrynus* or *Eophrynus*, where it is clear.

Piece *b* shows the ventral surface, the fourth left leg complete and other legs only as far as the end of the femur. All ten sternites can be seen (Figure 114), but the tenth is indicated only by the ends of the ninth sternite, as shown in the drawing by the solid lines. The anal operculum is very well preserved and both valves are visible. On the second sternite two faint impressions of lungs are present and between them a duct, opening between the second and third sternites and splitting into two finer ducts anteriorly is visible. The question arises as to whether the common duct is the uterus and the pair of branches the oviducts, or the ductus ejaculatorius and the vasa deferentia. The ducts are well visible even in the photograph shown in Figure 248. I am inclined to regard the specimen as a male, the ends of the fork, of course, representing the point at which the vasa deferentia were turned upward and backward. The ducts seem to be too slender to permit the passage of eggs. But there is no other evidence in support of either assumption. The arrangement of the coxae is also visible in the photograph and I tried to represent it more symmetrically in Figure 115. In the specimen only the right side shows clearly. In some places the ventral surface shows a few punctures, but generally speaking it makes the impression of being smooth or at most very finely granular. The measurements of the complete fourth left leg are as follows: femur 3.90, patella 2.43, tibia 3.14, metatarsus 1.29, tarsus 1.57, total 12.33. This shows that the fourth leg is fully three times as long as the carapace, slightly more than twice the ratio in *Cleptomartus* and *Cryptomartus*.

Specimen In. 1552, originally of the Johnson Collection from the Upper Carboniferous Coal Measures of Coseley, Staffs. Figure 40, 112, 243, 244 and 247. Two pieces. Piece *a* shows the dorsal surface, the pair of palpi complete, the first pair of legs complete and portions of other legs. Piece *b* shows the ventral surface of the abdomen complete except for a missing piece on the right side, the first and second pair of legs complete, the right third leg as far as the end of the metatarsus and the fourth legs as far as the end of the femur. The preservation is excellent and made it possible to reconstruct the entire specimen as shown in Figure 112, only the distal end of the fourth leg being copied from the one of the preceding specimen.

The dorsal surface is particularly important inasmuch as it shows the inside surface of the body wall including the soft membrane connecting the abdomen to the carapace and the diverging fibers of the dorsal longitudinal muscles which served to raise the abdomen. These muscle fibers are shown in Figure 40 and are so plainly visible that they are reproduced photographically in Figure 247. Instead of being parallel to each other, the fibers radiate to the right and left of the longitudinal axis. The constriction between the carapace and the abdomen is very distinct and here, on each side of the specimen, the fine outline of the connecting membrane is visible. Along the gently concave posterior edge of the carapace a row of deep punctures is situated. The surface of the carapace appears to be concave, with a median and some lateral convexities shown in Figure 112 by dots representing punctures. It is difficult to say whether this shape corresponded to the natural shape of the carapace in life, or is due to distortion, to uneven caving in of the surface in the process of fossilization. Pocock thought a similar appearance of the carapace in his type specimen to be structural. I am rather inclined to the other alternative, in which case the carapace had a surface more or less evenly curved in all directions. At any rate, compared with the size of the carapace the curvature was not great and the carapace was rather low. If Pocock's interpretation were accepted in the case of specimen No. 1552, there would be scarcely any room left for the accommodation of the muscles necessary to move such unusually stout limbs as the creature evidently possessed. My Figure 112 is based on exact measurements of length and width of each leg under microscope. In fact, I first made drawings under higher magnification with the aid of a camera lucida, transferred them to an equally enlarged drawing of the body and then reduced the drawing photographically to its present size. Figure 116 and 117 are made at a still greater magnification to show the details of structure. At the end of the tarsus of the first right leg a small claw is visible. Presumably it had a mate, but the latter is missing. The ventral edge of the femur, patella and tibia in the first and second pair of legs shows two pointed thorns each. The surface of the femur is smooth, but along its dorsal edge a single row of coarse punctures is visible. On the patella and tibia two rows of similar punctures are situated, each row in a conspicuous longitudinal groove, which must have represented a pair of parallel crests with a row of granules each. The punctures on the metatarsus of all legs are irregularly scattered over the

entire surface. The tarsus appears to be smooth. On the dorsal surface of the abdomen the punctures are arranged in rows as shown in Figure 112. The line between the ninth and tenth tergites is not visible, but on the ventral surface even the posterior edge of the ninth sternite is difficult to trace.

Total length 16.57 mm. Carapace 5.14 mm. long, 6.57 mm. wide in middle. Abdomen 11.43 mm. long, 4.57 mm. wide in front, 7.14 mm. wide about one third from posterior end.

Legs	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	5.00	3.86	4.29	1.71	1.57	16.43
II	4.00	3.43	3.57	1.57	1.50	14.07
III	3.57	2.43	2.57	1.57	1.50	11.84
IV	3.71	?	?	?	?	ca.12.85 (calculated)

Leg formula	1	2	4	3
	3.2	2.7	2.5	2.3

The length of the fourth leg was assumed to be equal to the combined lengths of the second and third, divided by half. This assumption is based on the measured length of the femur. The genital region is not well preserved.

Specimen In. 39769 from the Middle Coal Measures, Crow Coal, Phoenix Brickwork at Crowcreek, near Ryton-on-Tyne, Durham. Collected and presented to the British Museum in July 1940 by Wm. Eltringham. A single piece. Only the dorsal surface preserved. The anterior end and a piece of one side broken off. On the left, two coxae superimpressed over the carapace. The femur and base of the patella of a single leg preserved. It is difficult to determine whether it is the second or third right leg. The carapace cannot be measured, except its posterior, straight edge which is of the same length as the anterior edge of the abdomen. The abdomen is well preserved, but there is not one character by which one could determine whether this specimen represents a different species from the other two. It seems necessary to assign it to the same species, even though it was found in a much older formation.

Abdomen 11.2 mm. long, 4.6 mm. wide in front, 8.6 mm. wide about one third from posterior end. The shape of the abdomen and of the intersegmental lines is the same as in the preceding specimens and so is the distribution of the coarse punctures. The anal operculum is clearly superimpressed, is circular and shows both valves, the pos-

terior one smaller than the anterior. The femur is 5.3 mm. long. The specimen was evidently of about the same size as the others.

Anthracosiro fritschi Pocock

Geol. Mag. (4), 1903, Vol. X, pp. 450-408. Terrestrial Carboniferous Arachnida, 1911, p. 73, Fig. 37.

I have not seen the type of this species, represented by a single specimen. The Museum kindly sent me an electrotpe In. 14629 of a specimen accompanied by a label dated 6 Jan. 1912. According to this label the electrotpe was made from the original counterpart "mentioned but not figured in Geol. Mag. of December '11 by L. Moysey." The specimen was collected in Shipley, near Ilkeston, Derbyshire, Top Hard Coal, Jan. 1912. For the sake of completeness the photograph of the electrotpe, which came out quite well, is shown in Figure 249.

3. Family EOPHRYNIDAE Karsch

It is unfortunate that through some unaccountable error of my own I published a wrong figure of the abdomen of *Pleophrynus* on page 59 in my paper on Palaeozoic Arachnida of Illinois and, having been misled by my error, made the additional mistake of proposing a family *Pleophrynidae* characterized by the presence of only eight segments in the abdomen. As can be seen from the original photograph of the type specimen of *P. ensifer*, reproduced here in Figure 259, and from the corresponding Figure 121 showing the segmentation of the abdomen side by side with a photographic copy of Pocock's figure of *Eophrynus prestwicii*, enlarged to make it of the same size with that of *P. ensifer*, both have the same number of segments, nine. The only difference is in the absence of the segmentation line between the eighth and ninth tergites. In *Eophrynus*, according to Pocock, such a line is not present and he considers for that reason the entire plate as a single one. (The numbers in Figure 122 have been introduced by me for easier comparison with Figure 121.) In *Pleophrynus* that line is clearly visible. The Family *Pleophrynidae* becomes, therefore, a synonym of *Eophrynidae* and the genera which have really only eight segments had to be segregated in the new Families *Trigonotarbididae* and *Trigonomartidae*. The Family *Aphantomartidae* had also to be dropped, because the abdomen of *Aphantomartus*, as Pruvost has shown, consists of eight segments, and not of seven, as Pocock described and figured. In view of these important corrections and

changes it seems advisable to give here a new definition of the Family *Eophrynidae*.

Arachnida of the Order Trigonotarbi in which the abdomen is joined to the carapace only by the middle portion of the anterior edge. The first tergite much wider than the width of the juncture and as wide or wider than the posterior edge of the carapace. Nine abdominal tergites present, but the ninth may be fused without trace of a separation line with the eighth tergite, in which case the limit between the two is indicated by their sides at the point of the greatest constriction. The ninth tergite continues on the ventral surface between the arms of the greatly curved eighth sternite. On the ventral surface all nine sternites are present, the ninth with the anal operculum wedged in between the arms of the eighth sternite in front of the ventral portion of the ninth tergite. Carapace of a more or less triangular shape, with a pair of eyes or without eyes. Arrangement of coxae as in spiders. All coxae movable. A sternum and underlip present. Chelicerae two-jointed, retrovert. Pedipalpi pediform, six-jointed. Legs seven-jointed. Respiration apparently by means of four pairs of book-lungs situated on the second to fifth sternites.

Key to Genera of Eophrynidae

1. Posterior end of abdomen without spines, evenly rounded.
Carapace an equilateral triangle, the surface of which is subdivided into shallow hexagonal fields. Ninth tergite distinct. Eyes wanting. Ventral surface not known. Genus *Areomartus* Petrunkevitch.
- Posterior end of abdomen with two pairs of spines 2
2. Carapace sharply pointed, considerably longer than wide, with a pair of eyes on an eye-tubercle situated one quarter from posterior edge. Sides of carapace slightly concave. Genus *Pleophrynus* Petrunkevitch.
- Carapace wider than long, with convex sides 3
3. Carapace only a little wider than long, forming an almost equilateral triangle. Its surface elevated and distinctly sculptured, the postero-lateral corners rounded. Eye-tubercle in middle, but eyes wanting. Genus *Eophrynus* Woodward.
- Carapace much wider than long, sculptured, with postero-lateral corners angulate. Eye-tubercle with a pair of eyes in advance of middle. Genus *Kreischeria* Geinitz.

Genus *Eophrynus* Woodward, 1871Type *E. prestvici* (Buckland), sub *Curculioides*

Three species belong to this genus. They may be distinguished as follows:

1. Median tergal plates smooth. Last tergal plate with a distinct longitudinal median ridge. *E. varius*, n. sp.
- Median tergal plates coarsely granular. Last tergal plate without a longitudinal median ridge 2
2. Median tergal plates not subdivided, but each with four large tubercles in a transverse row. *E. prestvici* (Buckland) (Figure 122).
- Median tergal plates longitudinally divided by a pair of furrows. Large tubercles only on second tergite. *E. pococki* Gill.

The type specimen of *E. prestvici* was collected by W. Anstice at Coalbrook Dale, Shropshire. A second and much better specimen was found at Dudley, described by Woodward and later by Pocock in 1902 and by Fritsch in 1904 from plaster casts.

The type specimen of *E. pococki* was found in a clay-ironstone nodule from the Middle Coal Measures (Crow Coal) of Crawcrook, near Ryton-on-Tyne and is in the collection of Mr. William Eltringham.

Several species were at different times referred to the Genus *Eophrynus*, but do not belong to it. They are:

Eophrynus carbonis Howard and Thomas. It is the genotype of *Maiocercus* (q.v.).

Eophrynus salmii Stur was placed by Fritsch in his Genus *Stenotrogulus*.

Eophrynus sturii Haase was placed by Fritsch in his Genus *Cyclotrogulus*.

Eophrynus n. sp. Kusta was placed by Fritsch in his genus *Petroviccia* under the name of *P. proditoria*.

The genera of Fritsch are discussed above in the chapter on the Order Anthracomarti. Their status is uncertain and they must remain *incertae sedis* for the present.

Eophrynus varius n. sp.

Type and only specimen in the collection of the British Museum, In. 39767. It was collected by William Eltringham in the Middle Coal Measures, Crow Coal, Phoenix Brickworks at Crawcrook, near Ryton-on-Tyne, Durham, in 1940. Two pieces. Piece *a* shown in Figures 110 and 258 is the better of the two. It shows the dorsal surface of the abdomen and the femur of presumably the fourth left leg. The abdomen is not complete: the first and second tergites are missing and of the third only the greater part is preserved. The following tergites are all plainly visible and the two pairs of posterod spines stand out clearly. The two lines which separate the tergites into a median and a pair of lateral plates run along the top of a ridge with equally inclined sides and can be traced to the end of the seventh tergite. Between these two lines, on a lower level and parallel to each other two other lines can be seen. They correspond to the two inner lines of *Kreischeria*. But the shape of the abdomen reminds one more of that in *Eophrynus*. The outline of the 8 + 9 plate is not distinct, nor is there any indication of a line separating the two fused plates. Instead, the surface is covered with a network of pustules interrupted in the median line by a ridge reaching the end of the abdomen. The marginal plates are very wide, the distance between the longitudinal ridge separating the marginal from the median plate, measured along the intersegmental line between the sixth and seventh tergites is three quarters of the distance straight across between the two antero-lateral points of the seventh median plate. The median plates 3 to 7 are smooth, the slopes of the lateral ridges are shiny, the marginal fields, except for the portion forming the outer slope of the ridge are covered with a network of pustules which, in life, must have appeared as little fields separated from each other by a network of shallow grooves.

The length of that piece of the abdomen which is bordered in front by the intersegmental line between the third and fourth tergites, and behind by an imaginary line tangent to the inner pair of posterior spines is 12.8 mm., and assuming that the three anterior tergites were about as long together as the three following ones, the total length of the abdomen may be estimated at about 17.7 mm. The maximum width is 17.7 mm. The (?fourth) femur is ca. 9.7 mm.

Piece *b* is the reverse of piece *a*, but only three posterior segments and the femur are preserved. Ridges appear as grooves, pustules as flat tubercles. The intersegmental line separating the median seventh from the eighth tergite is very clear and straight, as are the posterior

edges of the marginal fields. The angle between the transverse and lateral portion of the intersegmental line is ca. 120° .

Genus *Pleophrynus* Petrunkevitch, 1945

Type *P. ensifer* Petrunkevitch

This genus is easily separable from *Eophrynus* by the shape of the carapace. Its characters, corrected as to the number of abdominal segments, are as follows:

Carapace triangular, longer than wide, with an eye-tubercle behind its middle, bearing a pair of eyes. Abdomen composed of nine segments. First tergite without marginal fields, but subdivided by a thin, transverse line into an anterior and a posterior half. The following seven tergites each with marginal fields. The seventh and eighth tergites with postero-lateral corners drawn out into pointed spines or thorns, so that the posterior end of the abdomen is not evenly rounded, but presents four spines. The ninth tergite is a single plate enclosed between the marginal plates of the eighth tergite on the sides and the median plate of the eighth tergite in front. The ninth tergite turns under at the end of the abdomen to the ventral surface and is enclosed here between the arms of the eighth sternite on the sides and the ninth sternite in front. The number of sternites is nine and they are all entire.

The arrangement of the coxae is shown in Figure 20, the segmentation of the abdomen in Figure 121 and the type of *Pleophrynus ensifer* in Figure 259. The genus is represented by a single species, the type specimen from the Pennsylvanian of Mazon Creek, Illinois, in the collection of the State Museum of Illinois.

Genus *Kreischeria* Geinitz, 1882

Type *K. wiedei* Geinitz

Geinitz gave a good description of the type which is represented by a single specimen from Zwickau, Germany. Pocock (111) referred to this genus a specimen from the Coal Measures of South Wales, which he described under the name of *Kreischeria verrucosa*. On page 78 he says: "The figures and description of the typical specimen of *K. wiedei*, published by Haase and Fritsch, are so irreconcilably discrepant that an accurate conception of the structure of the fossil is impossible. The species described below as new (i.e. *K. verrucosa*. A.P.) is certainly akin to that species, and I have decided on that account to refer it to the genus *Kreischeria*; but if the restoration of

K. wiedeii given by Fritsch is, as he claims, accurate, a new genus will probably have to be erected for *K. verrucosa*." I have compared the original drawing of *K. wiedeii* given by Geinitz (25) himself with Pocock's figure 40 of his *K. verrucosa* and consider it as certain that both belong to the same genus, unless the generic difference were based on the proportions and shape of the carapace, which cannot be done because of the imperfect preservation of the carapace in *K. wiedeii*. The somewhat fanciful drawings of Haase and Fritsch are the result of wrong interpretation of lines which have nothing to do either with abdominal segmentation or with the longitudinal subdivision of tergites.

Pruvost (115) transferred *K. verrucosa* in 1930 into my Genus *Trigonomartus* and included it in his key to the species of the latter. He did not take into account either the difference in the number of abdominal segments, or the fact that the last tergite of *Kreischeria* is without marginal fields and is fused with the median plate of the penultimate tergite and that the posterior edge of the abdomen is with four spines; while in *Trigonomartus* the last tergite has marginal fields, and the posterior edge of the abdomen is evenly rounded.

A third species, *Kreischeria thevenini*, was described and figured by Pruvost (113) on the basis of a single specimen from the "fosse Cuvinot d'Azin" in France. Because of a possibility of confusion of this species with *Hemikreischeria thevenini* Fritsch, which is a synonym of *Hemikreischeria geinitzi* Thevenin, Pruvost makes the following statement in a footnote on page 344: "Ce nom de *K. Thevenini* ne devra pas être confondu avec celui de *Hemikreischeria Thevenini* donné arbitrairement par A. Fritsch, précisément au fossile du bassin de Valenciennes décrit par A. Thévenin (*H. Geinitzi*) et rejeté ensuite ensuite par tous les auteurs comme synonyme de *H. Geinitzi*. C'est ici à un genre différent que j'applique à nouveau ce terme spécifique."

According to Pruvost his species may be distinguished from *K. wiedeii* by its much smaller size and by the relative measurements of the first tergite.

Genus *Areomartus* Petrunkevitch, 1913

Type *A. ovatus* Petrunkevitch

The type of this genus and species was described and figured by me (93) in 1913. It is shown here in Figure 123. It is represented by a single specimen found in the Pennsylvanian of the Fayette County

of West Virginia. It is No. 1196 of the U. S. National Museum. No other specimen has been found since its description.

4. Family TRICOGONOTARBIDAE, *new*

Characters of the family. Abdomen composed of eight segments, the last tergite without marginal fields, enclosed between the marginal fields of the seventh tergite and extending to the ventral surface where it is enclosed between the arms of the seventh sternite. Carapace triangular, high, with a pair of eyes. Juncture between carapace and abdomen occupying the full width of the first tergite. Second and third sternites with a pair of lungs each.

Two genera belong to this family. They can be separated as follows:

- a. Posterior end of abdomen evenly rounded. Carapace triangular, high, with an eye-tubercle bearing a pair of eyes. Legs similar. Genus *Trigonotarbus* Pocock.
- b. Posterior end of abdomen with four spines. Carapace not known, Fourth pair of legs much stouter and longer than the others. Genus *Hemikreischeria* Fritsch.

Genus *Trigonotarbus* Pocock, 1911

Type *T. johnsoni* Pocock

Pocock's definition of the genus contains only minor errors. The genus can be readily distinguished from other genera with the same number of segments, which are segregated here in the family *Trigonomartidae*, by the familial character of the last (eighth) tergite as given in the key to families of Trigonotarbi. The genus is at present restricted to its type species. The two American species *T. schucherti* and *T. carbonarius*, which I described in 1913 under the generic name of *Trigonotarbus*, do not belong to it. They will be found here under the generic name of *Lissomartus*, in the Family *Trigonomartidae*.

Trigonotarbus johnsoni Pocock

Terrestrial Carboniferous Arachnida, 1911, pp. 73-75, Figure 38. Plate III, figure 4.

This was evidently a common species in the Upper Carboniferous of Great Britain. Pocock mentions in addition to the type "many specimens in the Collections of Mr. Egginton, Mr. H. Johnson, and Mr. Madeley." Since he does not give further particulars concerning these specimens, it is difficult to decide which of the twelve specimens

sent to me for study by the British Museum belong to this lot. They are all from Coseley, Staffs. Figures 19, 104-111, 250-257.

Specimen In. 7695, originally of the W. Madeley Collection, purchased from Damon in July 1907. A single piece showing the ventral surface (Figure 251). Approximately 6 mm. long. All coxae are well preserved, those of the pedipalpi are as long as the first pedal coxae, but much narrower. Behind them the oesophagus appears in transverse section which is rectangular, wider than long and apparently indicates its composition of two plates.

Specimen In. 13911, from the J. S. Neil Collection, purchased 23 July, 1910. Two pieces. Total length 6.1 mm. Dorsal surface pressed out of shape on the right side of the nodule. The ventral surface shows the coxae and the sternum very clearly. The abdomen is incomplete, but the anterior sternites are very sharply outlined (Figure 257) and the first, triangular sternite is more distinct than in most specimens.

Specimen In. 13919, from the J. S. Neil Collection, purchased 23 July, 1910, is considerably smaller. Total length 5.0 mm. Two pieces.

Specimen In. 13921, from the same collection is still a little smaller. Total length 4.8 mm. Ventral surface shows only some coxal cavities. Dorsal surface is good and shows the eye-tubercle with both eyes.

Specimen In. 15859, purchased from J. R. Gregory in Jan. 1911. Two pieces, very well preserved. Piece *a* shows the dorsal surface and is unusual in having the basal joint of both chelicerae in front of the carapace. They are 1.29 mm. long, i.e. rather formidable for a specimen of only 5.9 mm. total length. Laterally compressed, the basal joints resemble the chelicerae of mygalomorph spiders. They are shown in Figure 104. The carapace is 2.43 mm. long, 2.86 mm. wide. Piece *b* shows the ventral surface. Both fangs are visible, the left one almost complete (Figure 105). The pedipalpal coxae are rather short and wide apart.

Specimen In. 15860, purchased from J. R. Gregory in Jan. 1911. Two pieces, very well preserved. Piece *a* shows the dorsal surface. Total length 6.5 mm. Piece *b* shows the ventral surface with all coxae, sternum and abdominal segments very clear. The coxae of the pedipalpi are short and separated by the narrow basal joints of chelicerae with a row of coarse punctures which were evidently tubercles in the ventral median line, as they are found also in some Recent mygalomorph spiders. The palpi are slender and long.

Specimen In. 15897, from the H. Johnson Collection, Purch. J. R. Gregory 25 Oct., 1913. Two pieces (Figures 106, 252 and 253). As the photographs show, it is an unusually complete and well preserved specimen. The shape of the carapace is preserved without distortion. The eye-tubercle, too small to show in the photograph, is easily recognizable under high power and the two eyes are clearly outlined. The palpi and most of the legs are in their normal position, but the rough texture of the soft matrix makes measurement of individual segments only approximate. Piece *b* shows the ventral surface with all five pairs of coxae plainly visible. The coxae of the pedipalpi are shorter than those of the first pair of legs and are separated from each other by the basal joints of the two chelicerae, clearly showing the row of coarse punctures in each. The fangs are not preserved. The most interesting feature of the ventral surface is the preservation of the lungs and of the intersegmental membranes. The first pair of lungs may be clearly seen at the ends of the second sternite. They not only have a different texture and slightly different color from the rest of the sternite, but are also with sharp outlines. The second pair situated on the third sternite is not as clearly outlined and may be seen only at a certain angle of incident light. But their color and texture resemble that of the first pair. By comparison with the size of the animal, the lungs are so small that one is inclined to suspect the existence of some other, auxiliary organs of respiration, such as ventral sacs or tracheal tubes. Possibly the two peculiar rows of paired tubercles visible on the intersegmental membranes are remnants of respiratory tubes or sacs. The ventral surface of this specimen gives an *inside* view of the body wall. The intersegmental membranes appear as distinct ridges with two tubercles side by side in close proximity on each side of four ridges. The two pairs of the intersegmental line between the third and fourth sternites are situated approximately in line with the lungs. The following two pairs slightly nearer to the axis of the body, the third two pairs about half way between the sides of the abdomen and the axis, the last two pairs, on the strongly curved last intersegmental line, are nearer to the axis than to the sides of the abdomen. They are visible in Figure 253 as somewhat lighter spots reflecting the light. The regular arrangement of the tubercles in two converging lines and the fact that they are visible in the same places on three other specimens is sufficient proof that we are confronted not with some freak of nature, but with regular structures. They cannot be attachments of dorso-ventral muscles. Such

attachments are visible in some fossil Arachnida and are, as in Recent ones, invariably on the sternites and not on the intersegmental membranes. Tracheal spiracles in Insects are usually on the sides of the dorsum. In Arachnida they are usually on the ventral surface and, at least in the case of the first pair of spiracles in apneumone spiders, they are in the line of the genital fold which corresponds to the intersegmental line. Ventral sacs of Arachnida of the orders Palpigradi and Phrynichida also open between sternites. But the fact that the tubercles are in pairs is more in favor of tracheal spiracles rather than evertible sacs. No double sacs are known in Recent Arachnida. On the other hand some insects have double spiracular openings, as for example the larvae of trypetid flies. The arrangement there is highly unusual, but it shows that duplication is possible. Personally I am inclined to believe that the structures in question are the inner ends of tracheal invaginations, although evidence in proof of this interpretation must wait for additional material.

Total length 6.3 mm. Carapace 3.1 mm. long, 3.5 mm. wide.

Legs	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	1.00	0.75	—	—	—	?
II	1.00	0.80	—	—	—	?
III	1.05	0.85	0.95	0.75	1.00	4.60
IV	1.25	1.10	—	—	—	—

Width of lung 0.450, height 0.275. Shape of first lung semicircular.

Specimen In. 31240, from Coseley, near Dudley, collected and presented by W. Egginton, Nov. 1932 (No. 8). Figures 107, 108, 250 and 254. Two pieces. Piece *a* shows the dorsal surface. Total length 5.7 mm. Carapace 2.71 mm. long, 2.71 mm. wide. Eye-tubercle approximately in middle; center of eyes 1.43 mm. from anterior end, 1.29 from posterior end. Diameter of eyes 0.20 mm. Distance between eyes almost equal to their diameter. Piece *b* shows the ventral surface. The first, triangular sternite is very sharply outlined. The lungs are broken off on both the second and third sternites.

Specimen In. 31241, from Coseley, near Dudley, collected and presented by W. Egginton, Nov. 1932 (No. 9). Figure 109. Two pieces. Piece *a* showing the dorsal surface is well preserved and the first leg is complete. Total length of specimen 6.0 mm. Carapace 2.57 mm. long, 2.57 mm. wide. First leg, femur 0.90, patella 0.72, tibia 0.77, metatarsus 0.40, tarsus 0.70, total 3.49. Second femur 0.70 mm., third femur 0.82, fourth femur 1.05 mm.

Piece *b* shows the ventral surface. The coxal region is well preserved, but the abdomen is damaged. The first right leg is as well preserved as on piece *a*. Of interest are the relative lengths of the trochanter and femur of the pedipalp, the trochanter being fully 0.50 mm. and the femur 0.75 mm. long. The patella of the second leg is 0.50 mm., the tibia 0.75 mm.

Specimen In. 31243, from Coseley, near Dudley, collected and presented by W. Egginton, Nov. 1932 (No. 11). Figure 255. Two pieces. Piece *a* shows the dorsal surface with the carapace badly compressed but the eyes very well preserved with the lenses fossilized and having the shape of beads. Total length 5.4 mm. Carapace 2.29 mm. long, 2.57 mm. wide (measured to middle and measurement doubled). Piece *b* shows the ventral surface, also distorted. The first sternite shows clearly its triangular outline. The lungs of the right side are broken off, but the left second lung is complete. The left first lung is not visible, because the edge of the sternite is folded over it. The place of the anal operculum occupied by a large lump, evidently representing the rectum.

Specimen In. 31254, from Coseley, near Dudley, collected and presented by W. Egginton, Nov. 1932 (No. 30). Two pieces. Figure 256. Piece *a* shows the dorsal surface with the carapace rather badly pressed out of shape, so that the eyes do not appear as distinct entities. Total length 4.0 mm. Carapace 2.0 mm. long, 2.0 mm. wide. Piece *b* showing the ventral surface is defective, but very interesting in one respect. The lungs of the right side are complete while the rest of the sternite is missing as shown in the photograph. On the left side both lungs are missing. The abdominal tubercles, supposedly representing the bases of tracheal tubes, are visible, but not very distinct.

Specimen In. 31255, from Coseley, near Dudley, collected and presented by W. Egginton, Nov. 1932 (No. 31), is represented by a single piece which shows the ventral surface. The specimen is not distorted, but neither is it as well preserved as some of the preceding ones, so that nothing of special interest can be observed. Total length ca. 6.1 mm.

Remarks concerning the characters of the species *T. johnsoni*.

Pocock's restoration of the dorsal surface in his Figure 38 is remarkably good. Nevertheless his description of the species seems to be incorrect in several respects which I wish to point out here. 1) The

eyes are separated from each other by about their diameter (Not contiguous, as Pocock states). 2) The abdomen shows clearly eight tergites, the seventh with marginal fields, the eighth entire, trapezoidal, narrower in front than behind, clearly separated from the median plate of the seventh tergite by a transverse line. Pocock overlooked this line and considered the median seventh plate together with the eighth as a single plate. 3) The tarsus is longer than the metatarsus, a peculiarity which it shares with *Anthracomarti*. 4) The number of sternites is eight; the eighth with the anal operculum on it, is followed by the ventral portion of the eighth tergite. The separation line between the two is sometimes visible, more often obsolete. 5) The first sternite is triangular. 6) A pair of lungs is present on the second sternite and another pair on the third sternite. 7) Four pairs of auxiliary organs of respiration, presumably tracheal tubes, are present on the fourth to seventh sternites. 8) The coxae increase in dimensions from the first to the fourth pair which is twice as large.

Genus *Hemikreischeria* Fritsch, 1904

Type *H. geinitzi* (Thevenin), sub *Kreischeria*

Hemikreischeria geinitzi is the only species. A single specimen showing only the ventral surface was found in Northern France. The latest description of this specimen is due to Pruvost (113) who published an excellent line drawing of it in 1919. This drawing is reproduced photographically in our Figure 129. According to Pruvost the number of *visible* tergites is seven, but he does not distinguish the eighth segment because the line between the seventh and eighth tergite is obsolete. We are confronted here with the same phenomenon as in *Eophrynus* and *Kreischeria*, except that in these two genera the vanished intersegmental line is between the eighth and ninth tergites, while in *Hemikreischeria* it is between the seventh and eighth. The characters of the genus are given in the key on the basis of Pruvost's description and figure, but with the above correction concerning the last *visible* tergite as being in reality a composite one.

Fritsch (23) described this species under the name of *H. thevenini*.

5. Family TRIGONOMARTIDAE

Abdomen composed of eight segments. Eighth tergite with marginal fields. Intersegmental lines more or less straight. Median plate of the eighth tergite ends at the posterior end of the abdomen and has no ventral piece. As now defined here, the family includes four

genera, one of which is new and had to be erected for two American species which were originally described by me (93) under the Genus *Trigonotarbus*. The Genus *Trigonomartus* was proposed by me in 1913, but at that time I did not fully realize the meaning of the tergal picture presented by it. The Genus *Phrynomartus* was proposed by me in 1945 and is retained here. The Genus *Aphantomartus* was placed by me in 1945 into a separate family, *Aphantomartidae*. My interpretation of the segmentation of the abdomen in *Aphantomartus* was based on Pocock's description and figure. Pruvost's description of *A. pococki* escaped my notice then. Now I have to accept Pruvost's statement that eight and not seven tergites are present. This means that the Family *Aphantomartidae* becomes a synonym of *Trigonomartidae*, the number of abdominal segments having served as the only character of distinction.

Key to Genera of Trigonomartidae

1. Posterior end of abdomen with two pairs of spine-like prolongations formed by the postero-lateral angles of the marginal plates of the seventh and eighth tergites. All median plates with two large tubercles, all marginal plates with a single large tubercle each. Genus *Phrynomartus* Petrunkevitch.
- Posterior end of abdomen without spines, evenly rounded . . . 2
2. Carapace distinctly sculptured. Abdomen either sculptured or else with flattened tubercles 3
- Carapace and abdomen smooth. Carapace subtriangular, slightly longer than wide, distinctly concave on each side near anterior end. Genus *Lissomartus*, new.
3. Carapace triangular, high, with a median crest in its posterior half. Eyes wanting. Surface of both carapace and abdomen covered with a network of fine ridges, with shallow polygonal depressions between them. Genus *Trigonomartus* Petrunkevitch.
- Carapace with larger, areolate sculpturing. Surface of abdomen with flattened tubercles. Eyes present. Genus *Aphantomartus* Pocock.

Genus *Trigonomartus* Petrunkevitch, 1913

Type *T. pustulatus* (Scudder), sub *Antibracomartus*

Four species belong to this genus. Two of them are North American

and two European. Pruvost placed in 1919 into this genus Pocock's *Kreischeria verrucosa*. We have seen above that that species has nine tergites and belongs to the Family *Eophrynidae*.

Trigonomartus pustulatus (Scudder), 1884, Proc. Amer. Acad. Arts, Sci. Vol. XX, p. 18 (sub *Anthracomartus*).

1890, Mem. Boston Soc. N. H., Vol. IV, p. 452, Plate 40, figs. 5, 8.

Petrunkévitch, Trans. Conn. Acad., 1913, Vol. 18, p. 102, figs. 60-62, Plate IX, figs. 47-51.

Pennsylvanian of Illinois. Three specimens. Figure 125.

T. woodruffi (Scudder), 1893. Bull. U. S. Geol. Survey No. 101, p. 9, Plate I (sub *Anthracomartus*).

Petrunkévitch, Trans. Conn. Acad., 1913, Vol. 18, p. 105, Plate IX, fig. 52.

Pennsylvanian of Rhode Island. A single specimen.

T. villeti Pruvost, 1919, Terrain Houiller du Nord de la France, p. 349, fig. 41.

1930, Faune continentale du Terrain Houiller de la Belgique, p. 207, Plate X, fig. 9.

Type from France, one specimen from Belgium.

T. dorlodoti Pruvost, 1930, La Faune continentale du Terrain Houiller de la Belgique, p. 208, Plate X, fig. 10.

Type from Belgium.

Genus *Lissomartus*, new

Type *L. schucherti* (Petrunkévitch), sub *Trigonotarbus*

Closely related to *Trigonomartus*, but carapace and abdomen with smooth surface.

Lissomartus schucherti (Petrunkévitch), 1913, Trans. Conn. Acad., Vol. 18, p. 106, figs. 63, 64, Plate X, figs. 53, 54 (sub *Trigonotarbus*). Mazon Creek Illinois. Figure 126.

L. carbonarius (Petrunkévitch), 1913, Trans. Conn. Acad., Vol. 18, p. 107, fig. 65, Plate X, fig. 55 (sub *Trigonotarbus*). Mazon Creek, Illinois.

Genus *Aphantomartus* Pocock, 1911

Type *A. areolatus* Pocock

Aphantomartus areolatus Pocock, 1911, Terrestrial Carboniferous Arachnida, p. 81, fig. 41, Plate III, fig. 6. Type from the Coal Measures

of S. Wales. Two other specimens from the same locality, according to Pocock.

A. pococki Pruvost, 1912, Ann. Soc. géol. du Nord, Vol. XLI, p. 96, Plate IV, figs. 5, 5a.

1919, Terrain Houiller du Nord de la France, p. 353, fig. 42.

A single specimen. Figure 127. France.

Genus *Phrynomartus* Petrunkevitch, 1945

Type *P. waechteri* (Guthörl), sub *Eophrynus*

With characters given in the key.

Phrynomartus waechteri (Guthörl), Senckenbergiana, 1938, Vol. 20, No. 6, p. 465-470, 3 figures. From the Coal Measures of the Saar.

The species is represented by a single specimen, the type, shown in Figure 128, which is a photographic copy of Guthörl's figure. The carapace, according to Guthörl, lacks eyes, is 5 mm. long and 6 mm. wide. As far as one can judge by the published figure and description, this species resembles not *Eophrynus*, as Guthörl claims, but rather *Aphantomartus*, with which it shares the presence of only eight abdominal segments, the eighth segment *with* marginal fields; but from which it may be easily distinguished by the characters given in the key.

IV SUBCLASS CAULOGASTRA

This subclass contains all Arachnida with a petiolate abdomen, i.e. such in which the first abdominal somite is reduced to a more or less slender pedicel. It is clear that this change of size and shape must have been accomplished in a manner very different from that found in Latigastrea. There a mere shortening of the first segment suffices. As long as the cavity in front and behind it remained sufficiently large to accommodate the organs normally belonging to the first somite, the shortening and even the disappearance of its outer wall would not be pregnant with grave consequences jeopardizing the existence of the animal. Not so in the case of the Caulogastrea. Here the volume of the internal space is tremendously reduced owing to peripheral constriction. The transformation of the originally wide first somite into a pedicel makes the fusion of the subsequent somites with the cephalothorax impossible. If the first somite should be lost

completely, the second somite would have to be transformed into a pedicel. That would involve serious difficulties because of the presence in the second somite of the lungs and of the openings of the genital organs. Indeed, the transformation of the second somite into a pedicel was accomplished only in the Ricinulei which have no lungs and whose tracheal spiracles are situated in the cephalothorax, above the posterior end of the third pedal coxae. Reduction through loss or fusion of abdominal segments in Caulogastra is limited to the abdomen and is independent of the cephalothorax with the exception of the central nervous system which becomes partly or completely incorporated in the thoracic ganglionic mass before the first somite is transformed into a pedicel. Thus the future evolution of Caulogastra has to follow totally different lines from those of Latiogastra. The Ricinulei must have early split off from the common ancestral stock. The loss of the first somite is their most important character. Apart from relatively small changes they had the same structure already in the Middle Coal Measures as they have today. The loss of the first somite must have preceded the formation of the cucullus and the development of the male copulatory apparatus on the third pair of legs. For these reasons I retain them here in the branch *Cucullifera*. The name is unfortunate, but was used previously and will serve for lack of a better one emphasizing the loss of the first somite.

The Solifugae may have also split off early from the common ancestral stock, if the two peculiarities of their structure may be considered to represent a primitive character. I have in mind the segmentation of their carapace and the presence of the anterior portion of the heart with two pairs of ostia in the cephalothorax. Yet the segmentation of the carapace occurs also in Palpigradi and Schizomida, which have very little in common with the Solifugae; and the extension of the heart into the cephalothorax is found in Thelyphonida. These two characters must have, therefore, originated independently in these orders. In looking over the structure of all organs in the entire subclass, I am inclined to believe that the structure of the mouth parts and the position of the mouth are features of fundamental value and presumably influenced an early splitting up of the subclass into branches. The condition found in Palpigradi and restricted to that order, must be regarded as the most primitive one. Here the chelicerae and the two lips alone serve as mouth parts. The pedipalpi have nothing to do either with ingestion or with production of

digestive enzymes and are used as legs. I propose for the Palpigradi the branch *Latisterna*, because it is the size of the anterior sternal sclerite which is responsible for the wide separation of the pedipalpal coxae and interferes with their becoming modified as mouth parts.

The branch *Camarostomata* is proposed here for the inclusion of the three closely related orders, Schizomida, Thelyphonida and Kustarachnae. The structure of the camarostome is described below. The camarostome is formed by the upper lip and the pedipalpal coxae, but these are modified in a way not found in any other group of Arachnida. The identity of the structure of the camarostome in now living Schizomida and Thelyphonida, and the considerable difference between these orders in other respects, such as the segmentation of the carapace and of the abdomen, the structure of the heart, of the organs of respiration etc., make it clear that the camarostome is the older character.

The Phrynichida and Araneae have many features in common, among them the structure of their mouth parts. These belong rather to the same type with that of the Palpigradi, but with the important difference that the pedipalpal coxae are approximated and definitely modified as maxillae. The name *Labellata* is proposed here for the branch including the Phrynichida and Araneae. It refers to the presence of lips without specifying the distinction of the mouth parts from those of the other orders.

Finally the branch *Rostrata* is proposed for the Solifugae, which alone among all Arachnida have the mouth at the end of a tubular beak formed by a fusion of the upper lip with the deutosternum.

The Caulogastra exhibit even better than the Latigastra the presence of primitive and modified characters in the same order. It is often difficult to decide, which character or group of characters should be considered of the ancestral type. Biologically the least important structures are often the ones which seem to persist, perhaps just because they are of no particular value. Their retention or loss would scarcely affect the life of an animal. On the other hand even a comparatively slight change in the structure of such important organs as mouth parts may mean the absolute impossibility of established ways of feeding and have great selective value. It is easy to see how changes of this kind, when of sufficient magnitude, could lead directly to the establishment of new, larger and to all appearance disconnected taxonomic units.

1. Branch *Latisserna*

Caulogastric Arachnida with a large, anterior, thoracic sternal plate which separates the pedipalpal coxae widely, effectively preventing their participation in a function as mouth parts. The latter consists only of the chelicerae and lips.

9. Order PALPIGRADI

Carapace segmented. Abdomen composed of eleven segments, the twelfth having disappeared and the ninth to eleventh forming a pygidium with a multi-jointed whip or flagellum. Mouth antero-ventral, with an anterior and a posterior lip. Pedipalpal coxae and the coxae of the first pair of legs widely separated by a large, single sternal plate. This is followed by three, much smaller sternal plates, one between each pair of legs and all rectangular in shape so that even the fourth pair of coxae is separated by the full width of the last sternal plate. Consequently, all coxae are movable and even the pedipalpal coxae have no gnathites. Chelicerae three-jointed, chelate, Pedipalpi slender, pediform, used in locomotion, and composed of a coxa, trochanter, femur, tibia, two-jointed metatarsus and three-jointed tarsus. First pair of legs tactile, longer and stouter than the pedipalpi, and composed of a coxa, trochanter, femur, patella, tibia, four-jointed metatarsus and three-jointed tarsus. Second, third and fourth pairs of legs composed of a coxa, trochanter, femur, patella, tibia, metatarsus and tarsus which is single-jointed in the second and third leg, but two-jointed in the fourth leg. All legs with a pair of claws. Midgut with simple diverticles in the abdomen. Heart in the abdomen, with four pairs of ostia. Coxal glands extend into the abdomen, their openings, one on each side, situated behind the first pedal coxae. Respiration presumably cutaneous and by means of evertible ventral sacs (two or three pairs) which have also a glandular function. Nervous system concentrated in the cephalothorax, with an abdominal ganglionic mass in the first two abdominal segments. Two families. Family *Koeneniidae*, Recent. Family *Sternarthronidae* Mesozoic and represented by a single species, *Sternarthron zittelli* Haase (= *Halomitra minor* Oppenheim) from the Jurassic of Europe.

2. Branch *Camarostomata*

This Branch includes three orders characterized by the possession of a camarostome, the floor of which is formed by a bowl-like depres-

sion in the common dorsal wall of the completely fused pedipalpal coxae, and the roof by the upper (anterior) lip. This arrangement is found in Recent Schizomida and Thelyphonida and is probably of the same kind in the Kustarachnae, though not actually observed here, except for the complete fusion of the pedipalpal coxae.

10. Order SCHIZOMIDA (= Pedipalpi Uropygi Schizopeltidia)

Carapace segmented (Figures 3 and 4). Abdomen composed of twelve segments, the last three annular, forming a pygidium with a short, 1- or 3-jointed telson. Pedipalpal coxae completely fused, line of fusion plainly visible, but cavity single. First pedal coxae wide apart (Figure 16), third pair contiguous. Second pair separated by a triangular sternal plate the apex of which is directed backward, fourth pair by a triangular metasternal plate, the blunt apex of which is directed forward. Posterior lip wanting. Mouth situated at the posterior end of the camarostome, above the coxae. Chelicerae two-jointed, chelate. Pedipalpi raptorial. First pair of legs tactile, without patella, but with a subsegmented, eight-jointed tarsus lacking claws. Second, third and fourth pair of legs with a patella and a three-jointed tarsus which terminates in an onychium with three claws in Recent species. Ventral sacs wanting. A single pair of lungs on second abdominal segment. Heart restricted to the abdomen with five pairs of ostia. Anterior four abdominal neuromeres incorporated in the thoracic ganglionic mass, the following neuromeres forming an abdominal ganglionic mass in the second abdominal segment. A single Recent Family *Schizomidae* and an extinct, Cenozoic Family *Calcitronidae* represented by a single species, *Calcitro fisheri* Petrunkevitch found in the onyx marble of Arizona. The two families are distinguished by the subsegmentation of their tarsal joints, the *Calcitronidae* having five joints in the second tarsus and four joints in the third and fourth tarsus. No other fossil records.

11. Order THELYPHONIDA

This Order corresponds strictly to the Division Holopeltidia of the Suborder Uropygi of the old Order Pedipalpi.

Carapace entire, with a doublure (Figures 1 and 2). Abdomen composed of twelve segments, the last three annular, forming a pygidium at the end of which is a long, segmented whip or flagellum. Pedipalpal coxae completely fused, line of fusion plainly visible, but cavity single. First pedal coxae small, widely separated (Figure 14).

Anterior sternal plate, separating the second pair of coxae, triangular, with its pointed apex directed backward. Fourth pair of coxae separated by a metasternal plate. Posterior lip wanting. Mouth situated at the posterior end of the camarostome, above the coxae (Figures 50-52). Chelicerae two-jointed, sub-chelate or retrovert. Pedipalpi powerful, raptorial. First pair of legs tactile, without patella, with a sub-segmented, nine-jointed tarsus, lacking claws. Second, third and fourth tarsi three-jointed, with three claws. Ventral sacs wanting. Two pairs of lungs, belonging to second and third abdominal segments. Heart with nine pairs of ostia, of which the two anterior pairs are situated in the cephalothorax, the other seven pairs in the abdomen. Eight pairs of median dorso-ventral muscles, each pair with attachment discs on the tergites and sternites of the first to eighth abdominal segments. Anterior seven abdominal neuromeres incorporated in the thoracic ganglionic mass, the following five neuromeres forming a single abdominal ganglionic mass in the eighth and ninth segments, connected with the thoracic mass by a pair of long connectives. A single Family *Thelyphonidae*, Recent and Palaeozoic, with the characters of the Order. It is a small family with something like ten Recent genera and a single palaeozoic Genus *Geralinura*. The characters used for the separation of Recent genera are not visible in fossils.

Family THELYPHONIDAE Lucas

Genus *Geralinura* Scudder, 1884

Type *G. carbonaria* Scudder

In view of the fact that the external characters used for the distinction of the Recent genera are not visible in fossils, we may characterize the Genus *Geralinura* as having the characters of the order and restricted to the Palaeozoic.

Up to the present five species of *Geralinura* have been described, three from the Pennsylvanian of Mazon Creek, Illinois, and two from the Coal Measures of Europe. These five species are listed in my Monograph of 1913 on page 59, with bibliographic references and synonymy.

Geralinura carbonaria Scudder is represented by a single specimen, the type, No. 37985 of the U. S. National Museum.

G. similis Petrunkevitch is also represented by a single specimen, the type, No. 1754-c of the same Museum.

G. gigantea Petrunkevitch was up to the present represented by two specimens: the type, No. 37976 of the U. S. National Museum

and the paratype, No. 147 of the Peabody Museum of Yale University. Recently Mr. George Langford of Joliet, Illinois, sent me a specimen of *G. gigantea* for examination. The specimen was collected by him in Mazon Creek and belongs now to his private collection. It is a well preserved specimen 20 mm. long, showing the typical features of the species as described and figured by me in 1913. In addition it shows clearly the anterior sternal thoracic plate of the same shape as in *G. similis* and five pairs of tergal attachment discs of the dorso-ventral muscles on the second to fifth tergites.

Geralinura bohémica (Kusta), the synonymy of which will be found on page 59 of my Monograph (1913), if that synonymy is correct, is represented according to Fritsch by the following nine specimens: six specimens of varying size, identified by him as *Prothelyphonus bohemicus*; one as *G. scudderi*; one as *G. noctua*; and one as *G. crassa*. It is possible that the type of the latter was lost and that Fritsch had really a different specimen before him (see Fritsch, Pal. Arachn. p. 62). The specimen from Chomle, which Fritsch mentioned on page 62 under the name of *Prothelyphonus* (?) *cordai* with a question mark and reproduced photographically in his text-figure 84 on p. 67 was overlooked by me in 1913 and does not appear in my list. Fritsch says that the specimen is only a fragment of the abdomen and gives no further description of it. From his figure it is impossible to decide whether it belongs to the Order Thelyphorida.

Geralinura britannica Pocock

Terrestrial Carboniferous Arachnida, p. 29, Plate I, fig. 3, Text-figure 9.

This species was up to the present known only from Pocock's description of the four specimens which he studied and none of which was complete. The whip is partly preserved in the type. The arrangement of the coxae is shown, as far as that was possible, in Pocock's text-figure 9 from the specimen in Madeley's collection. Of the specimens studied by Pocock, I have seen only his paratype, No. 49 of the Egginton Collection, now specimen In. 31265 of the British Museum, of which Pocock says on page 29 of his Terrestrial Carboniferous Arachnida that it shows "no features justifying its specific distinction from the type." In this respect I agree with Pocock, inasfar as such agreement is possible when it is based only on the description and figure given by Pocock. The specimen consists of two pieces which I subjected to cleaning. Piece *a* shows the dorsal surface

of the carapace and abdomen and short portions of several appendages. The total length of the specimen from the anterior end of the carapace to the end of the pygidium is ca. 22 mm. The carapace is 6.4 mm. long, 4.0 mm. wide, of the same shape as in the type. It is flat, widest in middle, with a straight posterior edge and rounded posterior corners. In the middle of the carapace a short longitudinal ridge is present, possibly corresponding to a groove on the outside surface, although it is difficult to decide whether the specimen presents a mold of the outer surface or a view of the inside of the carapace. At the anterior end, not far from the edge, a pair of round eyes are visible, but they are quite flat and the one on the right is not sharply defined. Lateral eyes cannot be seen. Piece *b* shows the ventral surface. The coxae are visible, but the sternum is not as well preserved as in specimen In. 7912. Of interest is the excellent preservation of the pygidium. It is cylindrical, with rounded posterior end. Its length is 3.30 mm., its width fully 1.43 mm. The first segment of the pygidium is twice as wide as long, its length being only 0.71 mm. The second segment is 0.86 mm. long and therefore also wider than long, although not to the same degree. The third segment is 1.73 mm. long, i.e. distinctly longer than wide. The flagellum is missing.

Specimen In. 7912 of the W. Madeley Collection from the bed of nodular ironstone about 10 feet above the thick or 10 yard coal, Coseley, Staffs., is, I believe, the specimen mentioned by Pocock on page 29 and shown in his text-figure 9, although there is no statement to this effect on the label. That there is a slight discrepancy between my measurements and those given by Pocock may be due to the fact that I cleaned the specimen thoroughly and exposed the pygidium. The specimen is slightly pressed out of shape and the abdomen lies at an angle to the cephalothorax. The specimen is shown photographically in Figure 265. Its total length is about 16.0 mm. The carapace is 4.60 mm. long, 3.50 mm. wide and shows clearly the median anterior point. The abdomen is 11.40 mm. long to the end of the pygidium. The shape of the carapace is the same as in specimen In. 31265, but no eyes can be seen. On the other hand, the median ridge is very well visible. Piece *b* shown in Figure 157, reveals the arrangement of the coxae and of the three thoracic sternal plates much better than even the American species, in which these structures are much more clearly visible than in the British specimens described by Pocock. If one compares the ventral surface of this Piece *b* with

the ventral surface of any now living representative of the Order Thelyphonida, one cannot escape the conviction that the ventral aspect of *G. britannica* is in every essential feature identical with that of the latter. Figure 14 shows the ventral surface of a male *Labochirus proboscideus* (Butler) from Ceylon, a rather aberrant type of a Recent whip-scorpion, in which the maxillary processes of the pedipalpal coxae are unusually developed. Yet the disposition of the coxae and of the sternal plates is the same. The study of Recent Thelyphonida shows that their fourth coxae are separated by the metasternal plate (Figure 14, MST), and that the first abdominal sternite is reduced in size to such an extent that it is scarcely visible, being hidden in the fold of the soft connecting membrane between the metasternum and the abdomen. Examination of specimen In. 7912 reveals the presence of a narrow transverse band of a slightly darker color than the rest of the abdomen, situated between what is evidently the metasternum and the second abdominal sternite. I think it is safe to assume that this band is the first abdominal sternite. Thus it becomes certain that the Palaeozoic Genus *Geralinura* possessed all the distinctive features of Recent Thelyphonida and that there is nothing in its structure that could suggest a more primitive condition.

The following key will be of help in separating the three American and two European species of *Geralinura*.

1. First abdominal tergite as wide as the carapace, so that there is no constriction between them. Carapace with convex sides, gradually converging to a blunt point. Fourth pair of coxae rectangular, contiguous in median line. *G. similis*.
- Between the carapace and the abdomen a distinct constriction. Fourth pair of coxae forming a triangle between them, occupied by the metasternum 2
2. Carapace egg-shaped, narrower in front than behind. Pygidium not sharply set off from the preceding segment, the sides of the latter continuous with the sides of the first pygidial segment. *G. carbonaria*.
- Carapace more or less of the shape of an elongated hexagon with anterior end narrower than posterior one 3
3. A pair of small, oval eyes present not far from anterior edge. a pair of deep, lateral crests extend from the anterior edge to a pair of tubercles situated not far from the sides of the

carapace and about two fifths of its total length form the anterior edge. *G. gigantea*.

— No lateral crests on the carapace 4

4. Carapace emarginate in front with a pair of eyes close to anterior edge. Adult about 30 mm. long to end of pygidium. *G. bohémica*.

— Carapace with a little pointed projection in front. Adult about 22 mm. long. *G. britannica*.

Judging by the photograph of the type of *G. bohémica*, reproduced in Fritsch's Palaeozoische Arachniden on page 60, it is the most complete of all specimens showing the body with the flagellum and three complete left legs and one right leg, as well as both pedipalpi. The first pair of legs is known only in *G. similis* and *G. gigantea*, but neither the American, nor the British species show the other legs complete.

12. Order KUSTARACHNAE

The complete fusion of the pedipalpal coxae along the mid-ventral line, without the slightest trace of their origin as a pair of joints, makes it quite certain that the mouth of the Kustarachnae is situated *above* the coxae, as in Schizomida and Thelyphonida. The unavoidable conclusion from this is that they must have also possessed a camaros-tome into which the mouth opened as in the two, just mentioned orders. The arrangement of the pedal coxae, however, is very different from that in Schizomida and Thelyphonida. They are triangular, in contact with each other and separated in the middle only by a minute sternum. Unlike the coxae of Phrynichida, the coxae of Kustarachnae were probably immobile. With the pedipalpal coxae completely fused, a posterior lip is naturally wanting. The known characters of the Order are few and may be summed up as follows:

Carapace entire, wider than long, evenly rounded in front, with a pair of eyes on an eye-tubercle. Abdomen segmented, ending in a small pygidium. Sterno-coxal region almost circular, with all coxae triangular, pedipalpal coxae fused into a single plate and the triangle between the fourth coxae presumably occupied by a metasternum. Chelicerae three-jointed, chelate. Legs long and thin.

Family KUSTARACHNIDAE

With the characters of the order.

Genus *Kustarachne* Scudder, 1890Type *K. tenuipes* Scudder

This being the only genus, its characters are those of the family. Three American Species belong to it. They may be distinguished as follows:

1. Carapace more or less crescentic, with posterior edge, strongly concave; eye-tubercle one third from anterior edge.
K. tenuipes.
2. Carapace with an almost straight posterior edge. Eye-tubercle almost in middle. *K. extincta*.
3. Carapace not known. Abdomen cone-shaped, without clear separation between the pygidium and the preceding segment.
K. conica.

Kustarachne tenuipes Scudder, Mem. Boston Soc. Nat. Hist., 1890, Vol. IV, p. 450, Plate 40, fig. 7.

Petrunkevitch, Trans. Conn. Acad., 1913, Vol. 18, p. 71. Text-figures 34, 35. Plate VI, figs. 33, 34.

The ventral surface of this species is shown in Figure 15, but the appendages are omitted. A single specimen, the type, from the Pennsylvanian of Mazon Creek, Illinois, in the U. S. National Museum.

Kustarachne extincta Melander, Journal of Geology, 1903, Vol. XI, p. 182, Plate V, fig. 4. Plate VII, fig. 5.

Petrunkevitch, Trans. Conn. Acad., 1913, Vol. 18, p. 73, Text-figures 37, 38.

A single specimen, the type, from Mazon Creek, Illinois.

Kustarachne conica Petrunkevitch, Trans. Conn. Acad., 1913, Vol. 18, p. 72, Text-figure 36, Plate VI, fig. 35.

A single specimen, the type, from Mazon Creek, Illinois.

3. Branch *Labellata*

Caulogastric Arachnida with mouth parts consisting of the chelicerae, pedipalpal coxae and two lips. Mouth antero-ventral, between the pedipalpal coxae. Posterior lip is either a deuto- or a trito-sternum.

13. Order PHRYNICHIDA

This order corresponds to the Suborder Amblypygi of the old Order Pedipalpi. Pocock was the first to give it the status of an order in "The Fauna of British India." The name was changed by me in 1945.

Carapace entire, without doublure. Abdomen composed of twelve segments, the last of which forms a pygidium. Telson wanting. Chelicerae two-jointed, retrovert. Pedipalpal coxae free, separated by the elongated prosternum (tritosternum) serving in place of a lower (posterior) lip. Pedipalpi raptorial. First pair of legs tactile, their coxae small, slender, wedged in between the pedipalpal and the second pedal coxae, patella present, tibia four-jointed, metatarsus multijointed and tarsus multijointed. Tarsus of second, third and fourth leg subsegmented, with three claws. A pair of ventral sacs present in the third abdominal segment. Two pairs of lungs, in second and third segments. Heart restricted to abdomen, with six pairs of ostia. Coxal glands with outlets either behind the first or behind the third pair of coxae. Abdominal neuromeres incorporated in the thoracic ganglionic mass. Even the external characters are so distinctive, that no Recent species of this order can be confused with spiders, which are their nearest relatives. This is true even in the case of the more primitive spiders belonging to the Suborder Liphistiomorphae in which the abdomen is also clearly segmented and consists of 12 segments. The distinction between spiders and Phrynychida is however not so simple in the case of fossil species. The characteristic first pair of legs, in Recent species so uniformly developed as tactile, feeler-like organs of considerable length, have not yet been observed in fossils for the simple reason that they break off so easily. Nor is a single case of a complete leg of any of the other pairs on record. Yet their structure, particularly the number of tibial and tarsal joints is used for the separation of Recent Phrynychida into three groups of familial or subfamilial value, *Phrynychidae*, *Tarantulidae* and *Charontidae*. The arrangement of the coxae and the structure of the sternal thoracic plates are rarely preserved without distortion. The absence of spinnerets should be sufficient to differentiate Phrynychida from Araneae, but spinnerets have not yet been seen in fossil spiders of the Palaeozoic era, except by Fritsch whose judgment in this respect may be doubted. Intersegmental lines, too, are not always plainly visible and the shape of the abdomen may make it impossible to see all twelve segments without rotating the abdomen, a condition evidently impossible when the entire abdomen is compressed as in the majority of fossils. If only the abdomen is preserved, it would not be an easy matter to decide whether it belonged to a spider, a phrynychid or a thelyphonid, and unless the legs are complete, the placing in a recognized family is impossible. One is, therefore, forced to do what is done in the case

of the Thelyphonida, i.e. disregard modern classification of Recent Phrynichida and use available characters for separation of strictly fossil genera.

Three genera of Carboniferous Phrynichida are known, *Graeophonus*, *Protophrynus* and *Thelyphrynus*. In 1913 I gave as the distinctive character of the Genus *Graeophonus* the presence of two joints in the trochanters. I think that I was misled by the presence of imprints of greatly distended trochantero-femoral interarticular membranes and now consider *Graeophonus* as having single-jointed trochanters, as all other Phrynichida. I am confirmed in this opinion by the examination of British fossils in which some legs show a similar condition, while other legs of the same specimen appear normal. Nevertheless the three genera remain distinct and may be separated as follows:

1. Carapace evenly rounded in front, without eyes. Coxae of third and fourth pair of legs only slightly widened distally and contiguous proximally along a median line. Genus *Thelyphrynus*.
- Carapace with a distinct frontal projection, with eyes. Coxae triangular 2
2. Anterior projection of carapace more or less nipple-like, eye-tubercle with a single pair of eyes. No lateral eyes. Ten or eleven tergites are visible. Genus *Graeophonus*.
- Anterior projection of carapace wide, with a pair of sessile eyes on it and another pair behind the projection, wide apart and marginal in position. Only seven tergites visible. Genus *Protophrynus*.

Genus *Graeophonus* Scudder, 1890

Type *G. carbonarius* Scudder

The genotype is represented only by two specimens, the type from the Pennsylvanian of Mazon Creek, Illinois (specimen No. 3085 of the collection of McGill University, Montreal, Canada), and specimen No. 37964 from the Upper Coal Measures, Joggins Mines, Nova Scotia, in the collection of the U. S. National Museum, Washington, D. C. The genotype may be distinguished from the British *G. anglicus* as follows:

- a. Carapace with a median crest in posterior half.
G. carbonarius.

b. Carapace without median crest, with radiating grooves.

G. anglicus.

***Graeophonus anglicus* Pocock**

Figures 161, 162, 263, 264 and 268

Pocock examined seven specimens and figured five of them. His description is very good, but the specimens did not show any complete leg. It seems that none of the six specimens which I refer to this species here belongs to the group of seven studied by Pocock. Five of his specimens, including the type, came from Coseley and two from South Wales. The six specimens now before me, are all from Coseley. Thus there are in all 13 specimens which belong to this species, showing that the species must have been fairly common in Great Britain in the Upper Carboniferous. In addition to these specimens there is one specimen, In. 39768 of the British Museum, from the Middle Coal Measures, Crow Coal, Phoenix Brickworks at Crowcrook, near Ryton-on-Tyne, Durham, which I refer tentatively to the Genus *Graeophonus*. Unfortunately it is a very incomplete specimen, a single piece, showing only the abdomen, probably the dorsal surface, but even that is not certain. There are seven tergites plainly visible. The pygidium, if there was one, cannot be seen, although something like a portion of it may be discerned in certain positions of the incident light. One sclerite in front of the main imprint of the abdomen may be a displaced tergite, and two curved structures on the right side of the specimen may also be displaced tergites.

Specimen In. 31257—labelled also as No. 34 of the W. Egginton Collection—is of special interest because of certain features which it shows clearly. It is represented by two pieces, one of which is shown in Figures 161 and 261. The abdomen is lacking. The carapace is well preserved, but the eyes cannot be seen. Three segments of both palpi are preserved and the terminal segment is visible on the other piece. There are two small spines on the femur, two much stouter and longer spines on the tibia, one at the end of the basitarsus. On the left side of the nodule the femora of the second, third and fourth leg are preserved; on the right a considerable portion of the left second and the complete left fourth leg. The coxae are visible on piece *b* which shows the complete leg still better. The trochanter is single-jointed, the basitarsus two-jointed, the tarsus four-jointed. The carapace

is 5.0 mm. long, 5.7 mm. wide. First femur ?, second 5.2, third 5.2. Fourth leg, femur 6.14, patella 1.29, tibia 5.86, basitarsus (1) 2.57, (2) 1.29, tarsus 1.14, total 18.29 mm.

Specimen In. 7905 is No. 58 of the W. Madeley Collection and is represented by a single piece showing the ventral surface of the abdomen, several coxae and three left femora. The abdomen is not complete and in its anterior portion dorsal intersegmental lines are superimpressed over the ventral ones, confusing the picture.

Specimen In. 7892 also of the W. Madeley Collection is represented by two pieces, both showing only the abdomen and that incomplete. However, on four of the segments on both pieces impressions of attachment discs of the dorso-ventral muscles are visible.

Specimen In. 13872, purchased from J. S. Neil, 23 July, 1910, consists of two pieces, also showing only the abdomen, but the latter is complete and beautifully preserved. Especially well visible are the lateral pleurae and four pairs of dorso-ventral muscular attachment discs.

Specimen In. 13877, like the preceding one purchased from J. S. Neil, 23 July, 1910, consists of two pieces. Piece *a* shows the carapace, the basal joints of the chelicerae, a portion of one segment of both palpi and two pairs of femora (Figures 162 and 263). The chelicerae are slender and parallel. The eye-tubercle is clearly outlined and both eyes plainly visible. Piece *b* (Figure 264) shows the ventral surface fairly well preserved, with part of the sterno-coxal region and the abdomen, also three pairs of femora. The approximate total size of the specimen is 9 mm. Carapace 3.7 mm. long, 4.0 mm. wide. Eye-tubercle hemispherical, 0.5 mm. in diameter. Eyes round, 0.22 mm. in diameter, separated from each other by about three quarters of their diameter. Lateral eyes wanting. Abdomen measured from anterior point of first sternite to posterior end 6.8 mm. long, 4.3 mm. wide. Second femur 3.5, third femur 4.2, fourth femur 5.0 mm.

Specimen In. 22836 of the Wheelton Hind Collection, 1921, consists of two pieces showing only the abdomen. The specimen is accompanied by a label stating that it is Pocock's paratype of *Plesiosiro madeleyi*, with reference to page 44 of his monograph. If it is true that Pocock had this specimen before him when he wrote the monograph, his error of identification can be explained only by insufficient cleaning of the surface. For when this was done by me, the abdomen revealed the characteristic features of a *Graeophonus* and none of a

Plesiosiro. The segmentation lines and five pairs of dorso-ventral muscular attachment discs are well preserved on both pieces. There is no median line dividing the segments, the pleurae are well visible and the shape of the abdomen is typical of *Graeophonus anglicus*.

General remarks concerning the species

It may now be accepted as definitely established that *G. anglicus* has a sharply defined hemispherical eye-tubercle bearing a pair of round eyes; a pair of slender, porrect chelicerae; powerful pedipalpi of the raptorial type, with two small spines on the femur, two large spines on the tibia and a single apical spine on the basitarsus. The segmentation of the walking leg is the same as in Recent species. The structure of the first leg still remains unknown.

Genus *Thelyphrynus* Petrunkevitch, 1913

Type *T. elongatus* Petrunkevitch

This genus and species are represented by a single specimen from Mazon Creek, Illinois, described and figured by me on page 66 of my Monograph.

Genus *Protophrynus* Petrunkevitch, 1913

Type *P. carbonarius* Petrunkevitch

Until recently this genus and species were represented by a single specimen from Mazon Creek, Illinois, described and figured by me in my Monograph on page 70. In 1930 Pruvost referred to this species a carapace found in the Coal Measures of Belgium. He gives a figure of the carapace on Plate XII showing both pairs of eyes and the general structure of the surface. His statement, that he is unable to find any character which would permit him to distinguish this carapace from the American specimen is certainly correct. Nevertheless I doubt very much that the Belgian fossil belongs to the same species as the American one. Both are incomplete, lacking many important characters of specific value. The characters of the American species are insufficiently known. Until new material in America and Belgium becomes available, the creation of a new species would be hazardous and undesirable.

14 Order ARANEAE

The spiders are too well known to require an account of their characters here. If any information concerning them were required,

it may be found in Kükenthal's Handbuch der Zoologie and in the Introduction to my Study of Amber Spiders. Nevertheless, a few remarks seem to be in place here, because of the peculiarities of fossil material in general and Palaeozoic fossils in particular. The two characters common to all spiders without exception and distinguishing them from all other orders of Arachnida are the spinnerets, present in both sexes, and the copulatory organs on the palpi, restricted to the male sex. Tertiary spiders possess both characters. Both the spinnerets and the palpi are clearly visible in Baltic amber specimens and in specimens preserved as imprints on Tertiary shale. While Recent spiders can be identified on the basis of their external structures alone, the principles of their classification involve the knowledge of internal organs, especially those of circulation and respiration. The heart is visible from the outside only in spiderlings and in very few species of adult spiders. The cardiac ostia can be seen and counted only under the microscope, when the heart has been removed and specially prepared. In no Tertiary spider is the heart preserved. The lungs are plainly visible from the outside in Recent spiders and the lung-spiracles are also visible, though not always as easily as the lungs themselves. In Tertiary spiders it is a very rare and exceptional case, indeed, when either the lungs or their spiracles can be seen. Tracheal spiracles are still more difficult to see in Recent spiders and the tracheal tubes, while visible in some species from the outside, require special methods of preparation for their study. The tracheal tubes have not yet been seen in Tertiary spiders and even the tracheal spiracles have been observed by me in only two or three cases. Thus even Tertiary spiders, notwithstanding their marvellous preservation, lack some of the most important familial characters.

The Mesozoic era has so far left not a single fossil representative of spiders. *Hasseltides* (*Hasseltia*) *primigenius* Weyenbergh from the Jurassic of Solenhofen in Bavaria, discovered in 1869, proved to be an opilionid and not a spider.

Palaeozoic spiders are, for some reason, not as well preserved as other Arachnida of that era. Complete palpi are not known and it is impossible to decide, therefore, whether the males of that distant age had already their copulatory apparatus on their palpi, or whether that peculiar character developed at some later period. Neither have spinnerets been seen either by Pocock or others except Fritsch. But Fritsch confused spiders with Anthracomarti and figured representatives of the latter order with abdominal appendages which they cer-

tainly did not possess. Similarly, he figured spinnerets in at least four spiders, but it is very doubtful that the structures which he interpreted as spinnerets really were spinnerets. Until his specimens have been re-examined by a trained arachnologist familiar with fossil material, it is wiser to disregard this character although it is quite certain, that spinnerets must have been present in all spiders.

Recent spiders are now generally divided into more than sixty families. In 1922 I proposed the Tertiary Family *Parattidae* for the inclusion of four species of *Parattus* from Florissant, Colorado, and in 1942 five Tertiary Families, *Arthrodictynidae*, *Insecutoridae*, *Spatiatoridae*, *Adjutoridae* and *Inceptoridae* for Baltic amber spiders. In 1913 I recognized a single family of Paleozoic spiders, *Arthrolycosidae*, and assigned three genera to the Suborder Arachnomorphia without placing them in any known family. In April 1923, in my paper On Families of Spiders I proposed a Family *Arthromygalidae*. In October of the same year Hirst described *Palaeoecteniza crassipes* from the Devonian, but did not assign it to any family and even put a question mark after the Order Araneae (?). Referring to the abdomen Hirst says: "it is impossible to be quite certain whether this is segmented or not." (p. 460.) At the end of the same paragraph Hirst adds: "It is possible that the spinneret-like structures shown in the figure are merely folds of the skin—on the other hand, they may prove to be true spinnerets." Reading Hirst's paper and looking at his figure of *Palaeoecteniza crassipes* I am unable to decide whether the specimen in question is a spider or belongs to another order of Arachnida. Leaving this question for future decision, when more material will be available, we may limit ourselves to a discussion of Carboniferous and Permian Araneae.

The distinction between the two families of liphistiomorph spiders, *Arthrolycosidae* and *Arthromygalidae*, was based by me on the structure of their eyes. From the point of view of modern arachnology that character alone is not sufficient for familial characterization. In some Mygalomorph spiders one finds in the same family spiders with eyes in a compact group on an eye-tubercle and such with eyes situated on the surface of the carapace, as for example, the Subfamilies *Leptopelmatinae* and *Sasoninae* of the Recent Family *Barychelidae*. The two Recent families of liphistiomorph spiders, i.e. of spiders with distinctly segmented abdomen, *Liphistiidae* and *Heptathelidae* have eyes on a distinct eye-tubercle. Of the Paleozoic liphistiomorph spiders only the American species of *Arthrolycosa* have eyes on an eye-tubercle. All European liphistiomorph spiders seem either to have eyes in two

rows on the surface of the carapace or are blind. An eye-tubercle is more easily preserved than sessile eyes. Consequently, while one may be certain that a fossil spider had no eye-tubercle, it is more difficult to decide whether sessile eyes were present or wanting. I believe that the presence or absence of an eye-tubercle still remains the only tangible character for the separation of the two families.

1. Family ARTHROLYCOSIDAE Fritsch (Petrunkevitch, 1923)

In 1923 I was inclined to refer to this family, with some doubt, the genera *Protolycosa* and *Eoeteniza*. The eyes of *Protolycosa* are not preserved, nor does Fritsch, who examined the type specimen, mention either eyes or an eye-tubercle. Of the eyes of *Eoeteniza silvicola* Pocock says: "This cephalic area bears the eyes, arranged in a transversely elongated, suboblong cluster, near its anterior border." He does not mention an eye-tubercle, nor does his figure on Plate II show any tubercle. Both American species of the Genus *Arthrolycosa*, *A. antiqua* Harger and *A. danielsi* Petrunkevitch show the eye-tubercle clearly. Both species are described and figured by me in my Monograph of 1913.

2. Family ARTHROMYGALIDAE Petrunkevitch, 1923

It seems that all European liphistiomorph Palaeozoic spiders belong to this family. The family includes the Genus *Arthromygale* Petrunkevitch 1922 (*A. carbonaria* Kusta, *A. fortis* Fritsch, *A. beecheri* Fritsch, *A. tarda* Fritsch and probably *A. lorenzi* Kusta and *A. palaranae* Fritsch, all from the Carboniferous), *Eoeteniza* Pocock, *Protoeteniza*, new, and possibly the genera *Rakovnicia*, and *Geralycosa* Kusta from the Carboniferous and the genera *Perneria*, *Pleurolycosa* and *Brachylycosa* Fritsch from the Permian.

Genus *Eoeteniza* Pocock, 1911

Type *E. silvicola* Pocock

Pocock established this genus on the basis of a single species represented by a single, incomplete specimen. The only tangible characters which he gives are the shape of the carapace with the head set off clearly from the thorax, the presence of eyes in a cluster near the anterior border and of six tergal plates in the abdomen. This last character has a peculiar interest inasmuch as in the specimen which I describe here below, only six tergites are present. Descriptions and

figures of European species of the Family *Arthromygalidae* all show either six or seven tergites. Of the two American species of *Arthrolycosa* one shows eight and the other six tergites. In two species of the Recent Genus *Liphistius*, which I have in my collection, only seven tergites can be seen from above, without turning the specimen. They are the third to ninth tergites, counting the pedicel as the first. The number of visible tergites may indicate greater or lesser convexity of the abdomen, but certainly has no generic value, is misleading and should not be employed in the definition of a genus.

Genus *Protocteniza*, new

Type *P. britannica* n. sp.

This genus differs from *Eocteniza* by the shape of its carapace and possibly by the absence of eyes which are not visible in the genotype. The head is not elevated, nor sharply set off. The carapace is longer than wide, widest in middle; gradually, but not much, narrowed anteriorly and posteriorly, and more or less flat. It resembles somewhat the carapace of *Geralycosa*, but the latter, according to Fritsch, is as long as wide.

Protocteniza britannica n. sp.

The type and only specimen *In. 14015* is from the Upper Coal Measures, Coseley, Staffs., was purchased from J. S. Neil, October 22, 1910, and consists of two pieces. Piece *a* shows the carapace and the abdomen, but only the proximal ends of the femora and the basal joints of the chelicerae. It is shown in Figures 158 and 262. Total length 5.0 mm. Carapace 2.3 mm. long, 1.85 mm. wide. The head is not recognizable as such, but there are two converging lines beginning on the outside of the chelicerae and meeting at a point just behind the middle of the carapace. The carapace is flat, with faint outlines of the coxae impressed on its surface. The more or less semilunar impression behind the coxae probably marks the position of the posterior declivity of the carapace. The abdomen is elliptic, 2.7 mm. long, 2.0 mm. wide. Six tergites are clearly visible. Piece *b* is very incomplete and shows faintly only the sternal region and the chelicerae, but the abdomen is missing.

It is possible that the specimen described by Pocock on page 34 as *Arthrolycosa* sp? belongs to this species, but the accompanying figure shows a broader carapace than the one in the type.

Arachnomorph Spiders

Pocock described an arachnomorph spider, *Archaeometa nephilina*, from the Upper Coal Measures, Coseley, and Fritsch described two arachnomorph spiders, *Pyritaranea rubifera* and *Eopholcus pedatus*, from the Permian. The latter two are shown only in line-drawings as restorations according to the explanatory statements of Fritsch himself. The characters of the genera are very inadequate. The type specimens should be reinvestigated before any judgment is passed concerning their status. Pocock's Genus *Archaeometa* is also very inadequately characterized. He begins its definition with the statement that it is "resembling in general form such Recent genera as *Nephila* and *Tetragnatha*, and possibly, like these, belonging to the family Argyropidae." (p. 36.) This resemblance is quite striking, but we must not forget that there are other spiders with more or less similar shape of the body, such as *Hypochilidae* and *Psecbridae*. *Nephila* and *Tetragnatha* belong to a rather advanced type of spider, whereas the *Hypochilidae* are much more primitive spiders from an evolutionary point of view. Representatives of the Recent Family *Dinopidae* also have a long abdomen and very long legs. They, too, must be regarded as more primitive than the *Argiopidae*, because they still possess the inner branches of the pleopods of the fourth abdominal somite, though modified as a so-called cribellum. Moreover, three species of *Dinopis*, with which I am acquainted at first hand, show faint segmental lines near the posterior end of their abdomen. These lines were shown by me in Figure 83 of *Dinopis lamia* from the West Indies, on page 235 of the second part of my Spiders of Porto Rico. Unfortunately, none of the familial characters are preserved either in the type of Pocock's *Archaeometa* or in the specimen which I refer to this genus and which is described below. Although the legs of the type specimen are incomplete, Pocock gives their probable order of length as 2431 on the strength of the length of the femora, a perfectly justified procedure. The order of legs in *Tetragnatha* is 1423, in *Nephila* 1243, in *Hypochilus* 1423 and in *Dinopis* 1243. Thus the order of legs in *Archaeometa* differs from that in all Recent spiders which it resembles.

According to Pocock, the "carapace (is) apparently cordate, narrowed in front." The carapace of *Nephila* is rather wide and high in front, that of *Tetragnatha* much flatter. The carapace of *Hypochilus* is quite flat and wide in front, as is the carapace of *Dinopis*. Thus the carapace of *Archaeometa* is also different from that of the Recent genera which it resembles.

The shape of the abdomen has at best generic value, but in many Recent spiders it varies considerably within the same genus and in some genera is strikingly different in the two sexes.

It is impossible to decide whether Fritsch's *Pyritaranea* and *Eopholcus* could be assigned to the same family with *Archaeometa*. It is also impossible to assign the latter to any Recent family, or to formulate the characters of a special family for its reception. But for the sake of convenience and because it is very improbable that *Archaeometa* could belong to any of the Recent families, I propose for it the Carboniferous Family *Archaeometidae* without any other definition than that it includes arachnomorph spiders of that geologic period.

3. Family ARCHAEOMETIDAE, new

Genus *Archaeometa* Pocock, 1911

Type *A. nephilina* Pocock

The type of the genus and species is, according to Pocock, a single specimen of the W. Egginton Collection. Figure 11, according to the accompanying explanation, is a "restoration of the ventral surface, showing the legs as far as the distal end of the femora and the probable form of the opisthosoma." In the text on page 36 Pocock says "Abdomen long, apparently longer than femur of fourth leg, but its exact length a little doubtful owing to the want of definition of its posterior end; subcylindrical in shape, a little narrowed posteriorly, ovally convex apparently anteriorly and rather more than three times as long as wide." The total length of the type specimen is given as about 10 mm.

Specimen In. 15863 of the British Museum, purchased from J. R. Gregory, Jan. 1911, comes from the same locality as the type, Upper Carboniferous Coal Measures, Coseley, Staffs., but seems to be better preserved. It consists of two pieces. Piece *a* shows the dorsal surface, with carapace and abdomen well preserved and clearly visible (Figures 159 and 260). Total length 12.4 mm. The carapace is very flat, 2.71 mm. long, 2.00 mm. wide, the width measured a little in front of the posterior edge which is straight. The sides of the carapace converge only slightly, as far as the level of the first coxae, then they become distinctly concave. Near the posterior end of the carapace a slight elevation is visible, probably corresponding to the dorsal apodeme known as thoracic groove and serving for the attachment of the dorsal dilator of the gizzard. The legs are not well enough

preserved to permit measurement and are for this reason shown without any indication of individual joints. The trochanters are unusually stout, reminding one of the legs of opilionids, rather than of Recent spiders. The abdomen is 9.7 mm. long, 2.55 mm. wide, with almost parallel sides and evenly rounded end. Four transverse lines can be seen near the end of the abdomen showing that the latter was still segmented in that region. At its end the anus is faintly outlined. A pair of longitudinal folds extend from the anterior end to the second transverse line. The surface of the body and legs is finely punctate and must have been granular in life.

Genus *Arachnometa*, new

Type *A. tuberculata* n. sp.

The difference between this genus and *Archaeometa* is in the shape of the carapace. It is more or less cone-shaped and much longer than wide. The abdomen is shorter, wider, constricted behind and devoid of segmental lines.

Arachnometa tuberculata n. sp.

Type. Specimen In. 13917—from the Upper Coal Measures, Coseley, Staffs., Purch. J. S. Neil, 23 July, 1910. Two pieces. Figures 160 and 261. A rather poorly preserved specimen. Total length 8.57 mm. Carapace 2.71 mm. long, 1.71 mm. wide, strongly converging toward anterior end, with slightly sinuous sides, but in general rather cone-shaped, quite flat. The abdomen is very different from that of *Archaeometa*. It is 5.86 mm. long, 3.15 mm. wide in its widest place. Both ends are rounded, but the anterior end is much wider than the posterior end. From the anterior middle point to about half its length the sides of the abdomen are convex, but from here on they are distinctly concave. The two longitudinal folds and the four transverse lines of *Archaeometa* are wanting in *Arachnometa tuberculata*. Instead, there are two tubercles in the median line, one behind the other and both connected by a median longitudinal ridge. The anterior tubercle or hump is surrounded by five radiating crests which appear like sharp, narrow grooves in the surface of the specimen. The mid-dorsal line of the abdomen shows a distinct dip downward behind the anterior hump, so that the abdomen must have had the shape somewhat resembling that of *Cyclosa caroli* or of *Terragnatha extensa*. The legs were undoubtedly long and thin, with the trochanter distinctly stouter than the femur.

The two British Palaeozoic arachnomorph spiders may be distinguished as follows:

- a. Carapace about one and one third as long as wide, with sides converging but slightly. Abdomen elongated, cylindrical, with a pair of longitudinal folds and four intersegmental lines at its end. *Archaeometa nephilina*.
- b. Carapace nearly two and two thirds as long as wide, much narrower in front than behind. Abdomen much wider in front than behind, without longitudinal folds or transverse lines, but with two tubercles connected by a median ridge. *Arachnometa tuberculata*.

NB. It would be hopeless to attempt the inclusion of any of Fritsch's species in a key, without a reexamination of the type specimens.

4. Branch *Cucullifera*

Caulogastric Arachnida with a cucullus at the anterior end of the carapace, for the protection of the mouth parts.

15. Order RICINULEI

Until recently the Order Ricinulei was known only from what could be learned by an examination of external skeletal structures. Now, however, we are fortunate to have some precise knowledge of their internal anatomy, owing to the investigation of Millot, published in 1945. To be sure, that newly acquired knowledge is far from complete. Nevertheless, a great deal has been gained toward the understanding of these highly specialized creatures which had all the essential features of their external anatomy already in the Carboniferous and must have already at that time possessed more or less similar internal structure.

Recent Ricinulei represent a very small group of rare Arachnida. In England and continental Europe they do not occur at all. In North America a single species has been described from Texas. All other known species are either from tropical Africa or tropical America. Distinguished from other Arachnida by a combination of characters, the Ricinulei possess two externally visible characters peculiar to that order and not found in any other order of Arachnida. One of these characters is present in both sexes and consists of a movable plate, the cucullus, attached to the front of the carapace and

turned under ventrally to protect the mouth parts when they are not in use. The other character is restricted to the male sex. It is the copulatory apparatus situated on the third pair of legs. All Recent Ricinulei belong to a single Family *Ricinoididae*, proposed by Ewing in place of Westwood's Family *Cryptostemmidae*.

Fossil Ricinulei have been found only in the Palaeozoic, where they are represented by two, now extinct families, *Polyocheridae* and *Curculioididae*. Both occur in North America and in Europe. Up to the present and including the two new species which will be described below, only thirteen fossil specimens of Ricinulei have been discovered, distributed over nine species.

In a paper entitled "La Constitution de l'abdomen des Ricinulei" Millot attempted to show that the Ricinulei have in their pygidium one annular segment more than the usually accepted number of three. He concludes on the basis of this discovery, that the abdomen of Ricinulei is composed of 10 segments, not counting the pregenital one, which seems to have disappeared completely. On page 72 he says: "Je crois pouvoir aujourd'hui élever ce nombre à 10, sans compter le segment prégénital qui, comme chez les Scorpions et chez les Opilions, semble avoir complètement disparu." He considers, in agreement with Hansen and Sørensen and their followers, that the crescentic anterior lip of the genital opening represents the first abdominal *visible* sternite, but interprets it as the sternite of the *second* abdominal segment and not of the *first*, as Hansen and Sørensen (39) apparently were inclined to do. At least in discussing this question, they say on page 120: "Thus the sexual orifice is here situated between the first and the second sternites, but in those orders to which Ricinulei are most nearly related, the sexual orifice is differently placed, viz. either in the posterior portion of the second segment (Palpigradi) or at the posterior margin of the second sternite (Pedi-palpi, Araneae). The question might therefore, fairly be raised whethere after all there may not also in Ricinulei exist one more segment in the abdomen, in front of those we have seen, in which case the sexual orifice would be placed behind the second sternite. We have had difficulty in examining this portion of the abdomen in *Cryptostemma*, but we do not consider the existence of such a further segment probable, because, in that case, the peduncle in Ricinulei would contain two entire segments, but this would be without a parallel in Arachnida with pedunculated abdomen; in some Araneae a portion of the second segment enters into the peduncle; but other-

wise only one entire segment is known to do so." I think it can be now accepted as certain that in all cases, in which the anatomy and development are known, the genital opening in both sexes belongs to the second abdominal somite. The only exception to this general rule is presented by some Acari in which the genital opening of the male is displaced dorsally and in *Demodex* is placed well forward on the cephalothorax. The very fact that such exceptions are limited to the male sex, while in the female the genital opening remains in its normal place, serves to emphasize the correctness of the accepted rule. There remains, however, the question as to the fate of the first abdominal somite in Ricinulei. In all other pedunculated Arachnida, the first abdominal somite, greatly reduced in size owing to peripheral construction, serves as a pedicel connecting the abdomen with the cephalothorax. A complete disappearance of the first somite is known only in Arachnida with broad juncture between the abdomen and the cephalothorax and is due not to peripheral constriction, but to shortening of the entire segment. Has the genital opening in Ricinulei been shifted forward one segment, to lie now between the first and second somites, or did the first somite disappear? In either case the Ricinulei present an exception to the rule. In other pedunculated Arachnida the disappearance of the first somite and its replacement by a greatly attenuated second somite is made impossible by the presence of lungs whose function would have to be taken over by some other arrangement. Only in Solifugae which have no book-lungs but only tracheal tubes, the second abdominal sternite has no spiracles, but even in their case the first somite, while greatly reduced, is still represented by a small, triangular tergite and a still smaller, triangular sternite, together forming the peduncular connection with the cephalothorax. In Ricinulei there are also no lungs. Respiration is by means of tracheal tubes and the only pair of spiracles is situated on the cephalothorax behind the fourth pair of coxae. Thus the disappearance of the first abdominal somite and the attenuation of the second, harboring no other important organs than the genital opening, would create no physiologically impossible situation. We have mentioned already that the tendency toward considerable diminution and ultimate loss of the first somite is general and common to all Arachnida. On the other hand a forward displacement of the genital opening is known only in Acari and here no peduncle is present and the limits between cephalothorax and abdomen are usually completely obliterated. Between the two alternatives the first one seems to me to be by far

the more likely. Only knowledge of developmental stages and neurological evidence can settle the problem definitely. Meanwhile we may accept that *the first somite disappeared* and that the first demonstrable tergite and sternite belong to the second embryonic somite. This means, of course, that in an uninjured, complete specimen examined from above, the anterior or first visible tergite is not the third, as usually stated, but the fourth. The last visible tergite is the seventh and not the sixth, and the pygidium is formed by the annular segments the first of which corresponds to the eighth somite. Whether the pygidium is composed of three, or as Millot accepts, of four segments, or whether only in some species a fourth segment is present, is not certain at present. Examining specimens of *Cryptocellus dorotheae* I can find only three segments. This is also confirmed by an examination of serial sections, transverse, frontal and sagittal. Palaeozoic Ricinulei with extrovert pygidium also show only three segments.

The palaeontologist, dealing only with external characters, may find it convenient to have external characters of Ricinulei pointed out here. The carapace is always entire, but with a movable anterior plate, the cucullus. Eyes are wanting. The abdomen is so coupled to the cephalothorax, that the actual juncture is not visible and the first visible tergite is the one which is usually labelled as the third, but belongs to the fourth abdominal somite. In Recent and some fossil Ricinulei four tergites are visible between the carapace and the pygidium. They are divided into three plates each by a pair of longitudinal lines. In some fossil Ricinulei the tergal plate of the abdomen shows no segmentation, but is instead divided longitudinally by a line which is not quite mid-dorsal in position. The arrangement of the coxae is different in Recent Ricinulei from that in fossil ones. In the former the second pair of coxae is contiguous in the middle line, while in both families of fossil Ricinulei the second coxae are separated by a sternal plate. The fourth coxae, which alone are movable, take part in the coupling of the abdomen, the third visible (fourth embryonic) sternite of which has special pouches for this purpose. The chelicerae are two-jointed, chelate. The pedipalpi are six-jointed, chelate. The trochanters of the first and second leg are single-jointed, those of the third and fourth leg two-jointed in Recent species. All tarsi are segmented, except the first which is single-jointed. The second and fourth are five-jointed, the third tarsus—four-jointed. A pair of claws present at the end of the tarsi are not visible except under microscope.

The tarsus and metatarsus of the third pair of legs in mature males are modified for purposes of copulation. Larva with only three pairs of legs.

Key to Families

1. Recent. First pair of coxae triangular and distinctly separated. Second and third pairs grown together with each other and along the median line. Tergites well visible, subdivided into three fields. Family *Ricinoididae* Ewing (= *Cryptostemmidae* Westwood) (Figure 21).
- Palaeozoic. Second pair of coxae separated by a sternal plate 2
2. Dorsal surface with four, clearly visible tergites, venter with four sternites. First pair of coxae contiguous in middle line. Family *Polyocheridae* Scudder (Figure 23).
- Dorsal surface of abdomen covered by a single shield divided by a median longitudinal line or without it. First pair of coxae either contiguous or separated. Venter of abdomen not segmented in two American species, segmented in British species, and the third, fourth and fifth sternites longitudinally subdivided by a pair of lines. Family *Cuculioideidae* Cockerell (Figure 22).

1. Family POLYOCHERIDAE Scudder

A single genus with the characters of the family.

Genus *Polyochera* Scudder, 1884

Type *P. punctulata* Scudder

Three species, two of which are American and one English. They may be distinguished as follows:

1. Carapace with gently converging, slightly convex sides, without appreciable constriction behind. *P. punctulata*.
- Carapace with strongly convex sides and deep constriction between it and the abdomen 2
2. Cucullus only little wider than long. Abdominal tergites with two pairs of round impressions each. *P. alticeps*.
- Cucullus much wider than long. Tergites smooth. *P. glabra*.

Polyochera punctulata Scudder. Described and figured in my Monograph in 1913 on page 78. Type No. 37971 of the U. S. National Museum, 15.5 mm. long, from Mazon Creek, Illinois. Specimen in the collection of Mr. L. E. Daniels, from the same locality. 12.5 mm.

Polyochera glabra Petrunkevitch, Type and only specimen No. 37981, in the U. S. National Museum, from Mazon Creek, Illinois.

Polyochera alticeps Pocock, 1911, *Terrestrial Carboniferous Arachnida*, p. 40, Plate II, figure 6. Text-figure 14. Type and only specimen in the W. Egginton Collection, from the Upper Coal Measures of Coseley, near Dudley.

2. Family CURCULIOIDIDAE Cockerell (= Holotergidae Petrunkevitch)

A single genus *Curculioides* with the characters of the family.

Genus *Curculioides* Buckland

Type *C. ansticii* Buckland

Three American and three European species.

Key to Species of *Curculioides*

1. Abdominal dorsal shield without median longitudinal line 2
 - Dorsal shield longitudinally divided by a line or ridge 3
2. Carapace as wide as long. *C. ansticii*, England.
 - Carapace wider than long. *C. sulcatus*, U.S.A.
3. Carapace as long as wide or very nearly so 4
 - Carapace much wider than long 5
4. Venter of abdomen with an unsegmented postgenital shield.
 - C. scaber*, U.S.A.
 - Venter clearly segmented and three of the sternites subdivided by a pair of longitudinal lines comparable to the dorsal lines in *Polyochera*. *C. gracilis*, U.S.A.
5. Third coxae much longer than wide. Surface of carapace even, uniformly punctate (granular in life). *C. granulatus* n. sp., England.
 - Third coxae as wide as long. Carapace with a median shallow groove and a pair of small pits in addition to regular punctures. *C. eltringhami* n. sp., England, Middle Coal Measures.

Curculioides ansticii Buckland

Bridgewater Treatise (ed. 2), 1837, Vol. II, p. 76, Plate 46, Figure 1.
Pocock, Terrestrial Carboniferous Arachnida, 1911, p. 39, Plate II, figure 7, Text-figures 12, 13.

The type was from Coalbrook Dale. Pocock studied three specimens from Coseley, near Dudley. One of these shown in Pocock's figure 13, of the W. Madeley Collection now belonging to the British Museum and labelled as In. 7885, is reproduced photographically in Figure 269. The portion of the body shown in Pocock's figure on the right side of the crack is not on the nodule any more, and was not there when the specimen came into my hands. Otherwise the specimen is still as figured and there is nothing that I can add to its description. I have not seen the other specimens described by Pocock.

Curculioides scaber (Scudder) and *Curculioides sulcatus* Melander were described and figured by me on pp. 82 and 83 of my Monograph in 1913. Each is represented by a single specimen from the Pennsylvanian of Mazon Creek, Illinois. *C. scaber* is in the collection of the U. S. National Museum (No. 37965); *C. sulcatus* in the collection of the Walker Museum of the University of Chicago (No. 9235).

Curculioides gracilis Petrunkevitch, was described and figured by me in the Palaeozoic Arachnida of Illinois, 1945. The Holotype No. 14862, is also from the Pennsylvanian of Mazon Creek and is in the collection of the Illinois State Museum.

Curculioides granulatus n. sp.

Figures 163-166, 266-267

Type, In. 18592 of the British Museum. Two pieces. (No. 26) Coal Measures. Shipley claypit. Presented by Dr. L. Moysey per H. Woodward, 1919.

Piece *a* shows the dorsal surface of the body and portions of six legs, the fourth left leg lacking only the tarsus. Piece *b* shows the ventral surface, the coxae, the first pair of legs to the beginning of the patella, the right second leg to the end of the tibia, the third left leg complete, the third right leg to the end of the femur and the fourth left leg to the beginning of the femur. Thus the specimen is more complete than the American species of this genus. The body is somewhat distorted on both pieces of the nodule, but not enough to cause any difficulty in interpretation of visible structures. To give a better

idea of the appearance of this species and thus to make its comparison with other species easier, the accompanying Figures 163 and 166 were corrected so as to avoid distortion and the legs are shown on both sides of the body, indicating restored portions by dotted lines. There is also in the specimen a transverse band between the carapace and the abdomen, caused by some portion of the body having been pressed against the back of the animal in the process of fossilization. It is omitted from the drawing. The posterior edge of the carapace is clearly outlined and shows that the posterior piece of the carapace is bent almost at right angles to the surface of the nodule. Similarly, the anterior edge of the abdomen is pressed down into the surface of the matrix. If both portions were straightened out, they would meet as shown in Figure 163. It will be noticed that the figure of the restored specimen has a striking resemblance to some insect, as indeed the story of the discovery of the first specimen of *Curculioides ansticii* shows, a resemblance responsible for the generic name. It is not impossible that in the genus *Curculioides* we are confronted with the earliest case of real mimicry, though the origin of the resemblance may have to be attributed to quite different causes. The line which corresponds to the inner edge of a wing of an insect, when the wings are folded, is not strictly median in position, nor straight, but somewhat nearer to one side of the abdomen and distinctly, though very slightly, curved. This shape and position of the longitudinal line is in favor of interpreting the species as a mimic of an insect, because most insects contemporary with it seem to have had wings of that shape, though somewhat wider posteriorly. In my Monograph the corresponding line in *Curculioides scaber*, shown there in Figure 47 on page 82, is represented straight and strictly median. I did that at the time because I was under the impression that the apparent asymmetry was due to distortion. In the photograph shown on Plate VII of the same Monograph the line is actually asymmetric. So it is in *Curculioides gracilis*, as may be seen in the photograph on Plate II of my Palaeozoic Arachnida of Illinois (1945). Even the scutellum of an insect is represented in *Curculioides granulatus* by the little triangle which appears in all three species of *Curculioides* as a swelling of triangular shape in its proper place at the anterior end of the longitudinal line. But does such remarkable resemblance of all species of *Curculioides* to an insect with folded wings mean that it was the result of natural selection either as a protection against some enemies or as a deception of innocent prospective victims of a

wily predator? I doubt it very much. The habits of Recent Ricinulei protect them sufficiently from larger enemies and do not expose them to view. The flat shape of the fossil Ricinulei and their general resemblance to Recent ones suggest strongly that their habits were similar to those of their now living relatives. It is true that the wrinkled state of the abdomen of fossil specimens speaks in favor of a comparatively soft skeleton. Nevertheless, the flat shape of their body makes them better adapted to life in surroundings in which such shape would be most useful, i.e. under rocks, in crevices, under bark or in the flat spaces between leaves and stem. But if, as I believe, such remarkable resemblance is not due to the kind of natural selection as supposed to be operative in cases of mimicry, then it would have to be regarded as the result of special parallelism due to the similarity of the chemo-physical structure of some constituent of the germ-cells. It makes one pause to consider the possibility of the operation of similar factors in other cases, generally regarded as true mimicry due to natural selection.

Description of the Type. Total length 16.5 mm. Cucullus 1.4 mm. long, 3.6 mm. wide. Carapace (without cucullus) 4.3 mm. long, 5.5 mm. wide. Probable order of legs 2134.

Legs	Femur	Patella	Tibia	Metatarsus	Tarsus	Total
I	2.86	—	—	—	—	?
II	6.14	1.86	4.72	2.57	?2.57	?17.96
III	2.43	2.86	2.86	1.86	2.57	12.58
IV	1.86	1.71	2.14	2.57	?2.57	?10.85

NB. The length of the second and fourth leg is given on the assumption that their tarsus is as long as the tarsus of the third leg. It is not likely that the difference in their length was sufficient to affect the total length appreciably.

Width of first femur 0.61 mm., of second femur 0.80 mm., of third femur 1.29 mm. and of fourth femur 0.86 mm.

The carapace is distinctly trapezoidal, narrowed in front almost to the width of the cucullus, widest a little in front of the posterior edge. The latter is very slightly procurved. The sides of the carapace are slightly convex and the posterior angles are distinctly rounded. The dorsal abdominal shield extends to the base of the pygidium. The sides of the abdomen are convex, evenly curved, and the pygidium is in direct continuation with the sides and not set off as in *C. sulcatus* and in all Recent Ricinulei. The pygidium is extrovert, as in *C. gracilis* and *C. eltringhami*, and is clearly composed of three seg-

ments, the first of which is of the shape of a truncated cone, a little more than twice as wide at the base as long (Figure 165). The second segment has also the shape of a truncated cone, but its base is only 1.5 times greater than its height. The third segment is cylindrical, about as wide as long. The "scutellum" is clearly visible. The longitudinal line is slightly curved and somewhat nearer the left side of the abdomen, giving the impression of a right elytra overlapping the left one. The entire dorsal surface, including the cucullus, but not the pygidium, is deeply punctate, i.e. was granular in life, a feature common in recent species.

The arrangement of the coxae, shown in Figure 166, is somewhat different from that in the American *C. gracilis* and *C. scaber*. The first coxae meet in a median line. Behind them is a triangular sternal plate with its apex directed backward. The second pair of coxae are triangular and much smaller than all the other coxae. They are widely separated by the anterior edge of the sternum. The coxae of the third pair of legs are subcontiguous at the apex of the sternum, but are otherwise separated by the sides of the latter. They are more or less rectangular, flat, 1.5 times longer than wide. The exact shape of the fourth pair of coxae cannot be determined because their posterior edge is partly concealed by the well developed locking apparatus of the abdomen. This apparatus, which in Recent Ricinulei consists of two pouches on the third (fourth embryonic) sternite, consists in *C. granulatus* also of two pouches with a curved posterior edge. In 1913 I figured them in *C. sulcatus* without realizing their nature, but simply speaking of them as "a strongly procurved fold." In *C. granulatus* the mouth of the pouch is clearly visible on the right side in the nodule, with the corresponding fourth coxa disappearing inside the cavity and thus leaving no room for doubt as to the identity of the fold. Behind the locking apparatus the venter presents three sternites divided longitudinally by a pair of lines, then a distinctly trapezoidal sternite which is not divided, and finally the three segments of the pygidium. This subdivision of the three abdominal sternites by a pair of longitudinal lines is almost identical with what I described in 1945 in *C. gracilis* and is particularly interesting, because the sternites of Recent Ricinulei, as well as those of *Polyocheiridae* are never divided longitudinally. The ventral surface of the body is minutely punctate, wherein it differs from the coarsely punctate dorsal surface.

Neither the chelicerae, nor the pedipalpi are preserved. The number of trochanters is the typical one for the order, i.e. the first and second

pair of legs have a single-jointed trochanter, the third and fourth pair a two-jointed one. Of the tarsi only the tarsus of the left third leg is preserved. This is of the greatest importance, for it is the only case of a fossil ricinuleid with a complete tarsus. It shows clearly four segments, the number typical for the third tarsus of all Recent species. This circumstance makes one suspect that the other tarsi will eventually be found also to follow the rule governing the segmentation of the tarsi in Recent species, when new material will be discovered. The relative length of the femur and patella of the third and fourth pair of legs is a rather unusual feature and especially noticeable when compared with the slender first and second pair of legs.

Curculioides eltringhami n. sp.

Figures 167-169, 270-271

Type and only specimen, In. 39771 of the British Museum, Middle Coal Measures, Crow Coal, Phoenix Brickworks at Crawcrook, near Ryton-on-Tyne, Durham. Collected and presented by William Eltringham, July 1940. Two pieces.

This remarkable species, a giant among the Ricinulei, is also the oldest representative of the order. Although far from being complete, the specimen is nevertheless sufficiently well preserved to show clearly many of the important characters. Its total length, when measured from the anterior end of the cucullus to the posterior end of the pygidium in the specimen as it appears in the nodule, is fully 23.5 mm. But the empty space between the well preserved posterior edge of the carapace and the coxae of the third pair of legs shows that the carapace was severed from the abdomen and displaced forward in the process of fossilization. Normally, judging by what is found in other fossil species, the anterior edge of the third coxae should correspond approximately to the middle of the carapace. If we make this necessary correction, the total length of the body would still be 21 mm., i.e. twice as large as that of the largest Recent species.

The carapace appears on both pieces, as do the legs, but on piece *a* it is deeply punctate and represents the mold, while on piece *b* it is granular and not quite complete. The abdomen, on the other hand, shows its dorsal surface on piece *a*, but its ventral surface on piece *b*. The cucullus is not complete, but its shape can be easily figured out from the preserved portion. It is 1.0 mm. long, ca. 4.0 mm. wide. The carapace is trapezoidal and without the cucullus is 5.72 mm. long and 6.43 mm. wide. Its surface is coarsely granular and is longi-

rudinally bisected by a shallow groove. A pair of small circular pits is present on the carapace three fifths of its length from the anterior edge, i.e. from the posterior edge of the cucullus.

The abdomen is elongated, with evenly curved, slightly convex, converging sides. The pygidium is extrovert, three-jointed, not sharply set off from the abdomen proper, but forming a slightly sinuous line with the end of the abdomen proper. The dorsal shield is not segmented, but is longitudinally bisected by an almost straight line which is slightly to the left of the plane of symmetry. On the ventral surface the locking apparatus is visible. This is followed by three sternites divided by a pair of longitudinal lines. The antepygidial sternite is not divided. It has strongly converging sides. None of the legs are complete, nor are the anterior coxae preserved. The first right leg is preserved as far as the end of its metatarsus, the second right leg to the middle of its tibia, the third right leg to the end of the femur, the third left to the beginning of its femur, the fourth right leg to the end of the femur and the fourth left leg to the end of the patella. Judging by the coxae of the third and fourth pair of legs the arrangement of the coxae must have been similar to that in *C. granulatus*, except that the third coxae are as wide as long. The number of the trochanterial joints is normal for the order. The third pair of legs are by far the stoutest, the first the most slender. First femur 5.5 mm. long, 0.71 mm. wide. Second femur 5.0 mm. long, 0.86 mm. wide. Third femur 3.6 mm. long, 1.43 mm. wide. Fourth femur 5.72 mm. long, 1.00 mm. wide.

The dorsal surface of the abdomen appears coarsely punctate, the ventral one finely punctate. The punctures of the third leg are shown in Figure 168.

5. Branch *Rostrata*

Caulogastric Arachnida with mouth at the end of a tubular rostrum.

16. Order SOLIFUGAE

Only one fossil representative of this order is known, *Protosolpuga carbonaria* Petrunkevitch, from the Pennsylvanian of Mazon Creek, Illinois, No. 155 in the collection of the Peabody Museum of Yale University. It is described and figured in my Monograph, 1913, on page 76. Those interested in the structure of Recent Solifugae will find ample information in Kästner's account in Kükenthal's Handbuch der

Zoologie, 1933, and a still more comprehensive and detailed treatment of the subject in Roewer's account of the order in Bronn's *Klassen und Ordnungen*, 1932-1934. A picture of the arrangement of the coxae is given in Figure 24.

GENERAL CONCLUSIONS

The present study, owing to the rich and well preserved material placed in my hands for study by the British Museum, has helped considerably in clearing up some problems of structure and relationship and raised interesting new questions concerning their origin, evolution, extinction of some orders and survival of other orders.

It seems to be now clear that already at an early geological age Arachnida split up into a number of orders, all exhibiting the same fundamental trend to a shortening of their abdomen through a loss of posterior segments and a loss, abbreviation or attenuation of the first segment. Studies of surviving orders show that these changes were accompanied by concentration of the neuromeres in a more or less compact mass. The fact that the trend is manifested by all orders makes it certain that it must have originated before the splitting up into orders. It is to a certain extent operative even at present as evidenced by the modifications found in Recent Arachnida. The same trend, only pushed to its extreme may be observed in Pycnogonida. But the nature of the trend, if considered entirely by itself, is one of simplification and loss, destructive of old characters, not constructive of new ones.

Superimposed over this original common trend toward simplification of structure through loss of certain portions of the body and its organs, which did not involve the loss of life, several other trends of a creative type are manifested in each order by a production of new characters. Some of these trends may be also of older origin than the splitting up of the class into orders, for they seem to be operative in several orders. Other trends, restricted to a single order, must have originated later. Such trends produce modifications clearly correlated with either the environment and manner of life, or with the physiology of the respective organs. Thus the flattening of the body and the torsion of limbs is directly correlated with the environment; the pumping and filtering apparatus of the digestive system with pre-digestion of food outside their own body; the rastellum of some mygalomorph spiders with their habit of burrowing; the position of the eyes and of their fields of vision with the character of the substratum of their environ-

ment and the mode of locomotion, etc. These creative trends leading to the formation of new characters and therefore to the formation of new genera and new species may and often do operate in direct opposition to the fundamental trend toward simplification. Thus the original primitive segmentation of the abdomen, visible in the Palaeozoic spiders of the genera *Arthrolycosa*, *Arthromygal*, *Eocteniza* and *Protocteniza* and in the Recent spiders of the Suborder Liphistiomorphae, was gradually lost in favor of an abdomen composed of only five somites and these without external signs of segmental lines. But in a great many Recent spiders of this type the abdomen developed a tendency to increase its volume by greater development of its dorsal surface, until it became so curved that it overlaps at least half of the carapace, impeding locomotion and requiring special conditions of life, and the development of special organs and patterns of behavior, such as spinnerets and webs; or until the back grew to the shape of a long posterior prolongation as in some *Theridiidae*, requiring a different correlation between structure and function. Subsegmentation of a segment of the body, such as we have already alluded to in the case of the scorpions, must also be regarded as a later trend than the loss of segments. Incidentally, the fact that it was manifested already in Silurian scorpions makes it quite impossible to consider the latter as ancestors of other orders of Arachnida. It may have a direct correlation with the use of the poison-gland and was possibly conditioned by the need of greater flexibility of the postabdomen, remembering that for purposes of stinging the latter is always raised and brought forward above the preabdomen. The fact that no other subsegmentation has ever been produced in scorpions, may be tentatively explained by the sufficiency of a single subdivision for complete correlation of structure and function.

It is interesting and important to note that those Arachnida which exhibit the least deviation from the original plan of structure, as far as one may judge by fossil remains, belong to orders with the greatest number of abdominal segments, Scorpiones, Thelyphonida, Phrynichida. It seems as if the fundamental trend of simplification was early checked in them, perhaps by an inability of further simplification without loss of life. Some modification in the arrangement of the coxae took place in Carboniferous scorpions and apparently led to early extinction of species possessing that modification. In Thelyphonida the arrangement of coxae in the Carboniferous *Geralinura britannica* is identical with that in Recent species. On the other hand, orders with a strong funda-

mental trend toward fusion and loss of segments, exhibit great modifications of structure. They are also, as a rule, more numerous and wider distributed. Witness Araneae, Opiliones and Acari. Each of these orders shows their own, distinctive types of modifications due to creative trends made possible by the particular structure of their bodies.

The question may be raised, was not the fundamental trend a special trend of a group of ancestral animals before that group split up into distinct smaller groups? In Arachnida a satisfactory answer to this question is difficult to find. Practically all organs exhibit only one trend common to all orders, the trend toward a loss of segments. This is true of the nervous system, muscular system, respiratory system, circulatory system and excretory system. The digestive system shows segmentation only in the midgut and here the trend towards a loss in the number of diverticles is apparent. Even appendages are subject to the same law of loss and not of increase in number. There are Acari with only two pairs of legs. Abdominal appendages disappeared in all orders except in scorpions (the combs) and spiders (the spinnerets). And even in the combs of scorpions a diminution in the number of teeth is noticeable, and in spiders a reduction in the number of spinnerets from four pairs to only one pair. As a matter of fact, the fundamental trend of fusion and loss of segments, and loss of appendages is much older than the Arachnida themselves, because it may be observed in all other classes of Arthropoda and even in Annelida. Are the fundamental creative trends non-existent or are they lost as soon as a group possessing them is split up into new, systematically smaller groups? And is that process repeated at each stage of evolution of new groups? Does so-called macroevolution never leave any evidence in the shape of characters newly produced in some manner before the disappearance of the trend which was responsible for their production? I do not think that these questions can be answered at present. Nor do I think that they can be answered solely by experimentation on living animals, as some experimentalists are inclined to believe. The time element is against it and cannot be disregarded unless long extinct modifications can be reproduced in the laboratory. Meanwhile we may search for evidence left by past geological eras, try to discover as many evolutionary trends as possible through a comparison of structural modifications of the same type, present in widely separated orders and by correlating the past with the present give a theoretical and yet reasonable picture of the course of evolution.

Using in this manner all the evidence now before us we may

thus briefly recapitulate the different steps in the evolution of arachnid orders as reflected by the trends in the modification of important structural characters. We may first assume the existence, probably in the Cambrian, of an ancestral arthropod stock in which the body was already composed of a cephalothorax and an abdomen broadly joined together. The trends toward displacement of organs and toward fusion and loss of segments were already present. Similarly the trend to adaptive modification of their appendages was also a fundamental attribute. Respiration was aquatic. The three divisions of the brain were distinct and the ventral chain of ganglia complete and segmentally normal.

The *first step* consisted in a change from the ancestral arthropod stock to an ancestral Chelicerate stock possessing the distinctive characters found in common to all classes of Chelicerata. In this stock the mouth must have already been displaced ventrally and posteriorly back of the first pair of remaining cephalothoracic appendages, which underwent an adaptive modification into chelicerae. The abdomen became restricted to twelve anterior segments. The deutocerebrum fused with the protocerebrum. Both the thorax and the abdomen still remained segmented.

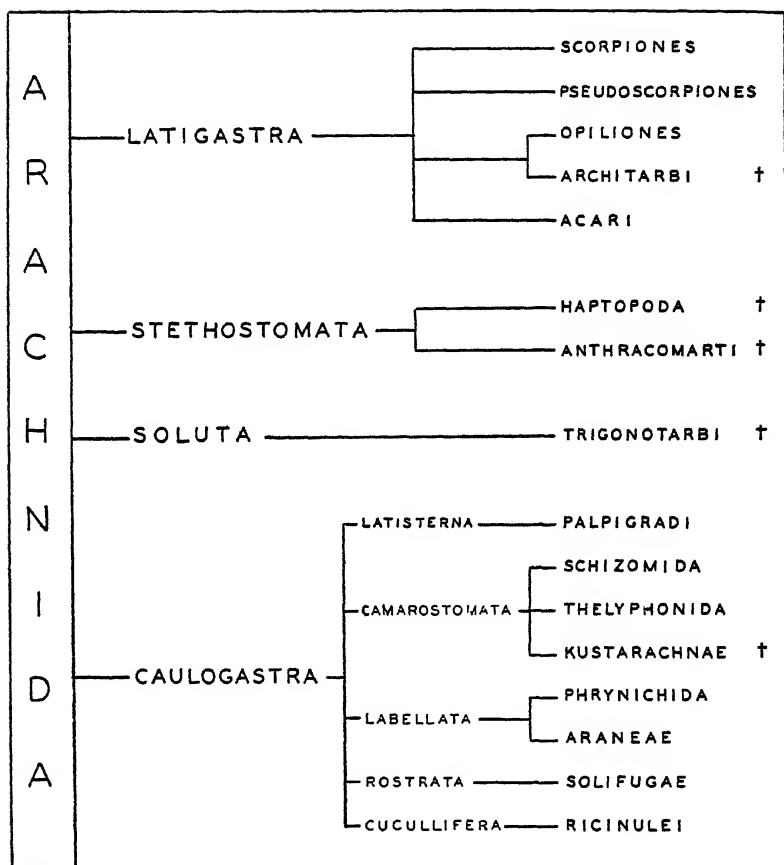
The *second step* consisted in the splitting up of the subphylum Chelicerata into four classes, Pycnogonida, Xiphosura, Eurypterida and Arachnida. The splitting probably was not simultaneous, but was complete in the Devonian. The old trends persisted, but new trends developed ushering in the *third step*. As we are interested here primarily in Arachnida, we may mention only briefly the other three classes. In Pycnogonida a proboscis with the mouth at its end was produced, the abdomen was reduced to a rudiment, the central nervous system became concentrated in the cephalothorax, etc. In Xiphosura and Eurypterida a carapace with a ventral doublure was produced and the mouth was displaced behind the pedipalpal coxae. The thoracic appendages were reduced to six pairs. In Xiphosura the first abdominal segment became incorporated in the cephalothorax and several posterior segments were lost, while the rest fused together. In Arachnida the abdomen remained segmented and complete, but respiration changed from aquatic to aerial and was accompanied by a loss of most abdominal appendages. The position of the genital opening became restricted to the second abdominal segment. The number of thoracic appendages became restricted to six pairs. Thus the ancestral arachnid must have resembled the ancestral eurypterid, but already differed from the latter.

We now shall consider the evolutionary steps which led to the splitting up of the Class Arachnida into sixteen different orders.

The *first step* involved the separation into four different lines of evolution which are therefore designated as subclasses. One change, the formation of the Subclass Stethostomata, was similar to that in Eurypterida and Xiphosura. It was the displacement of the mouth behind the pedipalpal coxae. This change was accompanied by the formation of an entire carapace, wedging in of the cheliceral coxae between the pedipalpal coxae, loss of the pedipalpal sternite and of the fourth pedal sternite and fusion of the first, second and third pedal sternites into a single sternal plate. Further changes representing the *second step* within this subclass led directly to the splitting up into two orders, Haptopoda and Anthracomarti. In the case of the Haptopoda the change involved less the abdomen than the appendages. The abdomen lost only one posterior segment and the book-lungs were restricted to two pairs. In the Anthracomarti the greatest change involved the abdomen. It lost two posterior segments, became considerably flattened and widened and presumably as a compensating adjustment developed longitudinal subdivision of its tergites and sternites.

The Subclass Latigastra retained another trend manifested by the Xiphosura, a trend to a fusion of the abdomen with the cephalothorax. This trend reached its climax in that branch of the subclass in which it was accompanied by a considerable modification of the mouth parts, and led as a second step to the production of three orders, Opiliones, Architarbi and Acari. The loss of the first segment in scorpions did not manifest itself until after the order was separated as such through subsegmentation of the eighth segment, formation of the tail, development of combs and of relatively enormous, chelate, grasping pedipalpi, all of which changes represent the second step. Modifications similar in nature led to the separation of the Order Pseudoscorpiones from the latigastric stock. In both these orders the trend to a loss of abdominal segments disappeared with the formation of the order. In the Pseudoscorpiones the abdomen underwent the least change, at any rate in regard to its segmentation. But the organs of respiration changed from book-lungs to tracheal tubes.

The Subclass Caulogastra was produced by a new trend consisting in a transformation of the first abdominal segment into a relatively small and slender pedicel through peripheral constriction. The splitting up of this subclass into five branches involved the appearance of several new trends. The trend to further loss of anterior segments led



PHYLOGENY OF THE ORDERS OF ARACHNIDA

only to the formation of the Order Ricinulei and was accompanied in this case by a number of other peculiar modifications. In the other four branches the operation of this trend was arrested. Modifications of the mouth parts seem to have been primarily responsible for their separation. The formation of a camarostome produced the branch which then split up into the Orders Schizomida, Thelyphonida and Kustarachnae. The development of a beak correlated with a change in the arrangement of the coxae and of the organs of respiration to tracheal tubes and accompanied by secondary segmentation of the carapace and invasion of the cephalothorax by the heart led to the formation of the Order Solifugae. The modification of the pedipalpal coxae into movable maxillae with the retention of the mouth between them produced the branch Labellata. In its Order Phrynichida the access to the mouth became restricted by the formation of a pair of converging furrows on the maxillae. The abdomen retained its twelve segments, but the twelfth segment was reduced to a pygidium. The pedipalpi became powerful raptorial organs and the first legs changed into antenna-like tactile organs. In the Order Araneae the maxillae developed digestive glands, the palpi of the males the copulatory apparatus. The abdomen produced spinnerets, developed the trend to a loss of segmentation, etc. Finally the Subclass Soluta which produced the Order Trigonotarbi seems to have attempted to combine trends which were separately produced by the other three subclasses, but which in combination proved to be lethal. Such combinations were: anthracomartid abdominal trend with caulogastric juncture and labellate mouth parts (*Eophrynidae*); latigastric abdominal trend and juncture with caulogastric coxo-sternal region (*Anthracosironidae*); anthracomartid abdominal trend with latigastric juncture and caulogastric coxosternal region (*Trigonotarbiidae*). This subclass was apparently incapable of producing new trends.

SUMMARY

1. The external and internal structure of Palaeozoic Arachnida is discussed on the basis of new evidence derived from a study of the collections of the British Museum. The peculiarities of fossil material are pointed out in detail and anatomical features compared with such found in Recent Arachnida.
2. The identity of the first abdominal segment is established in Haptopoda, Anthracomarti, Trigonotarbi, Architarbi and Scorpiones.

3. The backward displacement of the cheliceral coxae and of the mouth, comparable to that in Eurypterida and Xiphosura, is demonstrated in the case of the *Plesiosironidae* and *Anthracomartidae*, for which the Subclass Stethostomata is proposed.
4. The structure of the mouth parts of Recent Arachnida is discussed and the stomotheca of the Cyphophthalmi and the camarostome of the Schizomida and Thelyphonida described in detail.
5. The sterno-coxal region of the Architarbi is compared with that of the Cyphophthalmi and its interpretation corrected. The disappearance from view of the pedipalpal coxae in Architarbi is explained by their displacement dorso-posteriorly.
6. A new Order Trigonotarbi is proposed for Arachnida previously considered to be Anthracomarti, but which have an arrangement of coxae and a structure of mouth parts similar to what is found in Araneae. Because of the unstable condition of the type of juncture between the cephalothorax and the abdomen, the new Subclass Soluta is proposed for them.
7. The presence of a single pair of book-lungs in *Anthracosironidae*, of two pairs in *Trigonotarbiidae* and *Plesiosironidae* and of three pairs in *Anthracomartidae* is established and the lungs shown photographically.
8. Apodemes for the insertion of pulmonary muscles are described and figured.
9. Sexual characters are described in Anthracomarti in the shape of the genital atrium on the second sternite and of a depression on the third sternite, presumably for the housing of some accessory sexual glands or receptacles. The structures are compared with corresponding ones in whip-scorpions, to which they have the greatest resemblance in this respect. Up to the present, sexual differences remained unknown in Palaeozoic Arachnida.
10. The genital opening is described and figured in *Anthracosiro*.
11. The presence of eleven abdominal segments is established in Haptopoda.
12. The presence of ten abdominal segments is established in all Anthracomarti. The fusion of the second and third tergites into a single plate is demonstrated. The nature of the longitudinal

lines is elucidated and the presence of sternal marginal fields established. The structural plan of the anthracomartid abdomen is elucidated and the interpretation of previously misunderstood features in all genera of Anthracomarti brought in line with the plan.

13. The status of the type of *Anthracomartus völkelianus* is discussed, the later confusion pointed out and the specimen represented by Karsch's figure 1 reestablished as genotype.
14. The presence of ten abdominal segments in *Anthracosironidae* is established, and the disappearance of the first tergite demonstrated.
15. The broad connection between the cephalothorax and the abdomen is demonstrated in Anthracomarti, and in *Anthracosironidae* and *Trigonotarbidæ* among the Trigonotarbi. A band of longitudinal dorsal segmental muscle fibers has been found in the region corresponding to the first tergite in *Anthracosiro*, inserted in the posterior edge of the carapace and the anterior edge of the second tergite. These muscle fibers are figured and photographed.
16. The presence of eight segments in the abdomen of *Trigonotarbus* is demonstrated.
17. The identity of the sterno-coxal region in *Geralinura britannica* with that of Recent whip-scorpions is definitely established.
18. The segmentation of the posterior end of the abdomen in *Archaeometa* is described and figured.
19. The structure of the chelicerae of Haptopoda is described and figured.
20. The segmentation of all tarsi of Haptopoda is described and figured.
21. The segmentation of the third tarsus in *Curculioides* (Ricinulei) is described and figured.
22. The locking apparatus in fossil Ricinulei is described and figured.
23. The claws are described in *Anthracosironidae* and Anthracomarti. A claw of the latter is photographed.
24. The lateral eyes in two species of Palaeozoic scorpions are measured, figured and photographed.

25. A new classification is proposed, based on evolutionary trends which are discussed in detail. The Class Arachnida is subdivided into four subclasses on the basis of the juncture between the cephalothorax and the abdomen and the backward displacement of the mouth.
26. The true nature of the Silurian scorpions is discussed and a new classification of Palaeozoic scorpions proposed. The order is subdivided into two suborders: The Protoscorpiones, characterized by the presence of eight preabdominal segments, and Euscorpiones, in which the first segment disappeared and which include all Carboniferous scorpions with the exception of *Mazonia*, and all Recent scorpions.
27. Eight new genera of Palaeozoic scorpions are proposed and keys given to all families, genera and species of fossil scorpions.
28. The Order Architarbi is redefined, a new Genus *Mesotarbus* proposed and keys given to genera and species, including a separate key to British species which cannot be placed in recognized genera because of a lack of necessary data in their published descriptions.
29. A new definition of the Order Haptopoda is given on the basis of newly discovered facts, and the species *Plesiosiro madeleyi* is described in detail and figured.
30. A new definition of the Order Anthracomarti is given, with keys to genera and species. Pocock's species *A. hindi* and *A. priesti* are redescribed, figured and photographed. The true shape of their carapace is established. A new Genus *Cleptomartus* is proposed for two species which are described in detail.
31. *Anthracosiro woodwardi* and *Trigonotarbus johnsoni* are redescribed. The status of insufficiently described European species is discussed. A new species of *Eophrynus* from the Middle Coal Measures of Britain is described and figured.
32. A new genus and species of Araneae, *Arachnomata tuberculata*, from the Coal Measures of Britain is described.
33. Two new British Palaeozoic species of Ricinulei, *Curculioides granulatus* and *C. eltringhami*, are described and figured.
34. The subdivision of the Subclass Caulogastra into five evolutionary branches is proposed on the basis of the structure of their mouth parts.

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PLATES 1 - 52

PLATE 1

FIGURE 1. The carapace of *Mastigoproctus giganteus* (Lucas), a North American representative of the Order Thelyphonida. It is a typical example of a carapace consisting of a single, not segmented plate which is discarded as such at each moulting. ME - median eyes. LE - lateral eyes. TAP - thoracic apodeme for insertion of dorsal dilators of the gizzard. TS - thoracic sulci representing last vestiges of embryonic segmentation.

FIGURE 2. The same carapace viewed from below after removal of all adhering soft tissues. The doublure, i.e. the ventral fold of the carapace is represented by the striated area (DB). It is present only in the Thelyphonida among the Arachnida, but is a characteristic feature of the carapace in Eurypterida and Xiphosura.

FIGURE 3. The carapace of *Schizomus crassicaudatus* (Cambridge), a representative of the Order Schizomida from Ceylon. It is a typical example of a segmented carapace composed of five plates. PP - propeltidium. MSP - mesopeltidium. MTP - metapeltidium.

FIGURE 4. The same carapace viewed from the right side. CH - chelicera. P - pedipalp. 1 - 4 pedal coxae. MSP - mesopeltidium. MTP - metapeltidium.

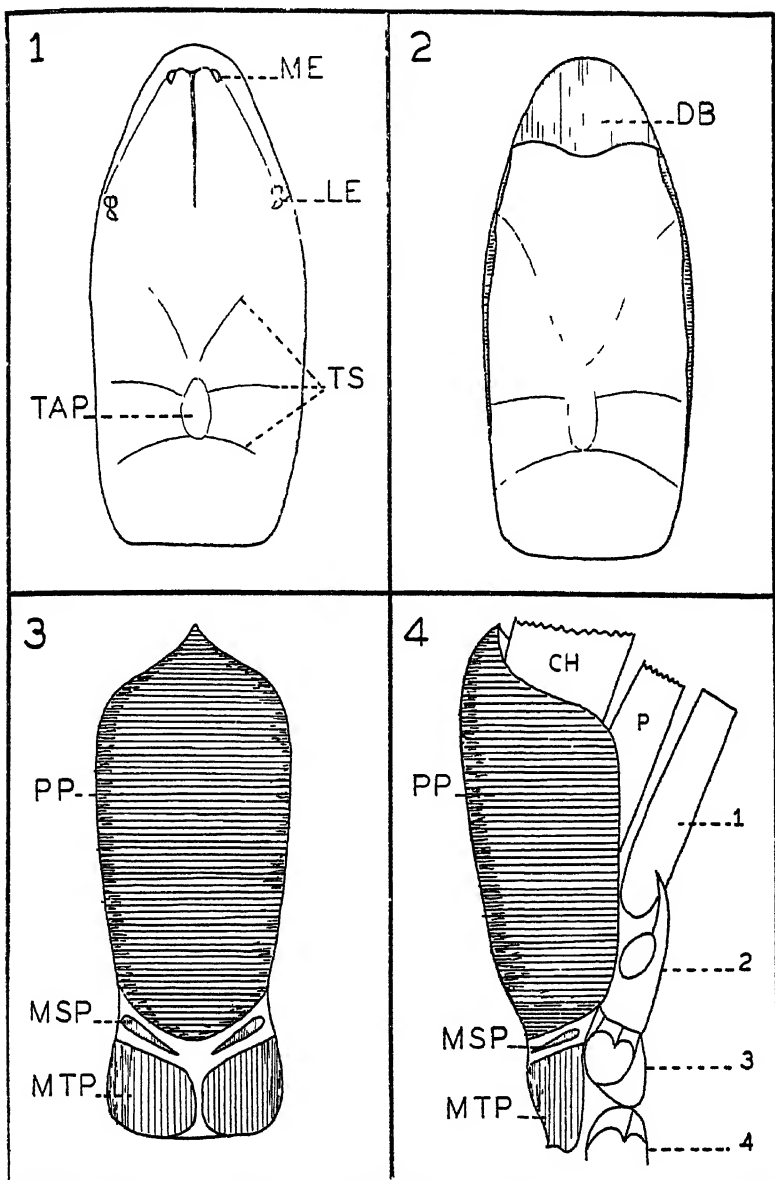


PLATE 2

The coxo-sternal region in Arachnida

FIGURE 5. *Diplocentrus scaber* Pocock — a representative of the Order Scorpiones from Jamaica, W. I. Pedipalpal coxae free. First and second pedal coxae free and supplied with gnathites. Third and fourth pedal coxae of each side permanently fused with each other and with the abdominal wall, movable only jointly and very slightly. GO - genital opening (in scorpions with a pair of opercula). P - pedipalpal coxae. 1 - 4 - pedal coxae. ST - sternum. 3S - sternite of the third abdominal somite (middle piece of combs).

FIGURE 6. *Chelifer cancroides* (Linnaeus), a cosmopolitan book-scorpion, a representative of the Order Pseudoscorpiones (Cheloneti). All coxae only very slightly mobile. Gnathites are wanting.

FIGURE 7. *Ixodes ricinus* (Linnaeus) — a cosmopolitan tick, a representative of the Order Acari with movable coxae. The specimen shown in the figure is one of normal size. In a specimen gorged with blood and abdomen greatly distended, the coxae are much farther apart. A - anus.

FIGURE 8. *Lebertia porosa* Sig Thor, a European mite of the Order Acari with fused coxae incorporated in the ventral body wall and forming plates known as epimera.

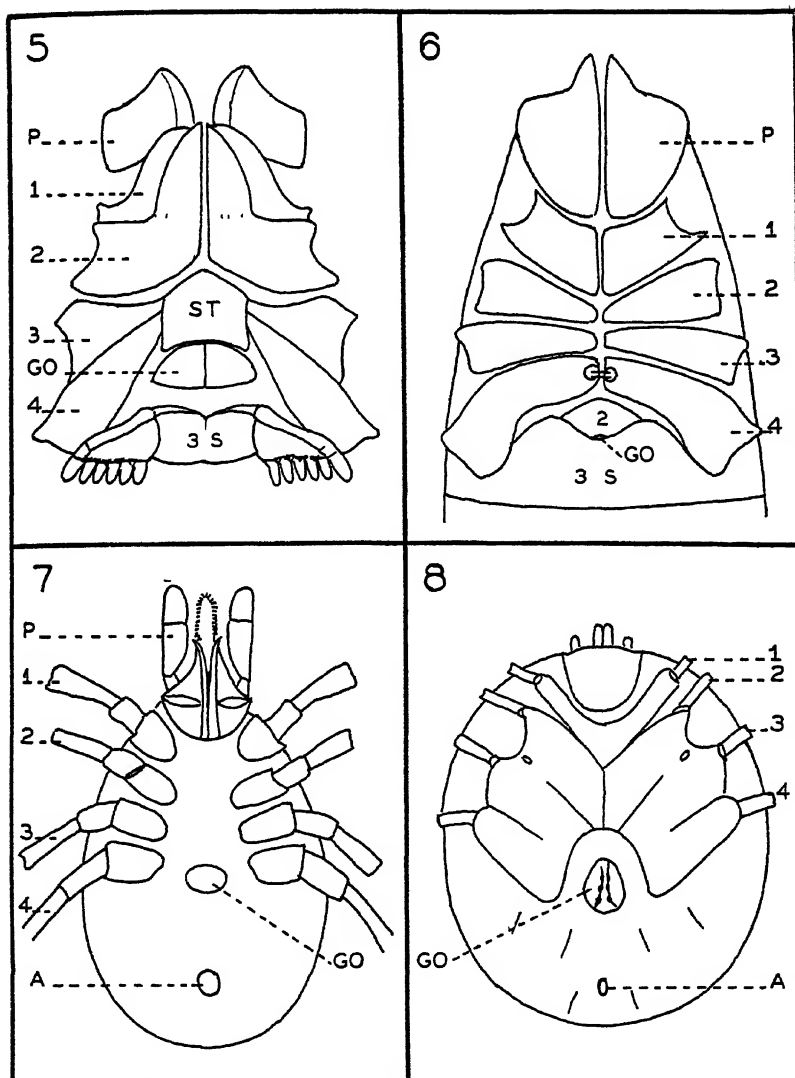


PLATE 3

The coxo-sternal region in Arachnida

FIGURE 9. *Opilio parietinus* (De Geer), a European harvestman, a representative of the Suborder Palpatores of the Order Opiliones, with all coxae movable. The coxae of the pedipalpi and the first and second pedal coxae with gnathites. CH - chelicera. P - pedipalp. 1 - 4 - pedal coxae. M - mouth. GO - genital operculum. R - upper (anterior) lip or rostrum.

FIGURE 10. *Phareicranaus calcariferus* (Simon) a harvestman from Trinidad, a representative of the Suborder Laniatores of the Order Opiliones. The pedipalpal coxae are movable and have gnathites. So are the first pedal coxae which also have gnathites. The other coxae are immobile, those of the fourth pair representing an extreme case of complete fusion with each other and with the abdominal wall along their posterior edge. SP - tracheal spiracle.

NB. in this and the following figures the trochanters are also shown.

FIGURE 11. *Stylocellus thorellii* Hansen and Sørensen, from Sumatra, a representative of the Suborder Cyphophthalmi of the Order Opiliones. The figure is a copy of H. and S.'s figure 6a on Plate II, but with omission of all shading. Second pedal coxae fused with the third coxae and immobile, the other coxae movable. In the Genus *Siro* of the same Suborder all coxae are movable. 3S - Sternite of third abdominal somite. 9S - Sternite of ninth abdominal somite.

FIGURE 12. *Architarbus minor* Petrunkevitch, a North American representative of the extinct Order Architarbi. The coxae of the pedipalpi are hidden behind the first pedal coxae which are apparently movable, although meeting in the median line. The dotted line on abdomen shows the outline of the carapace.

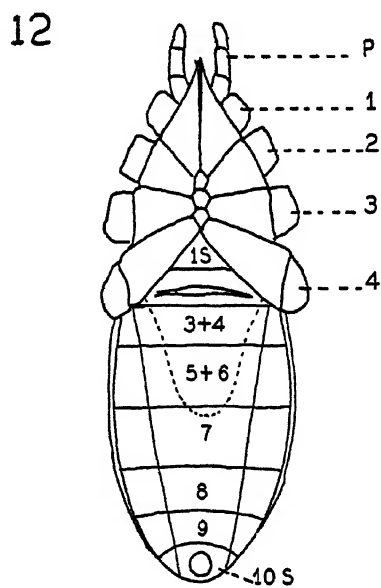
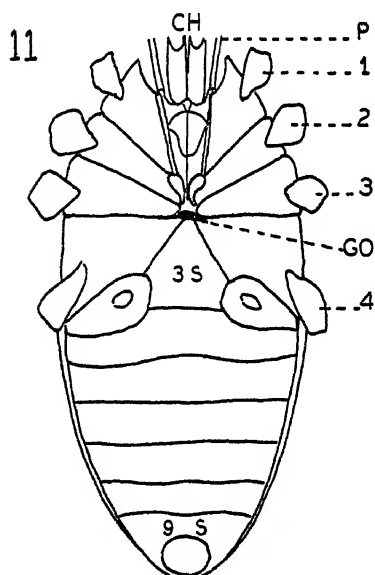
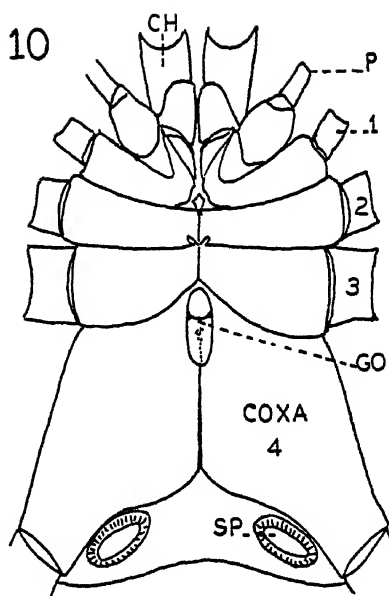
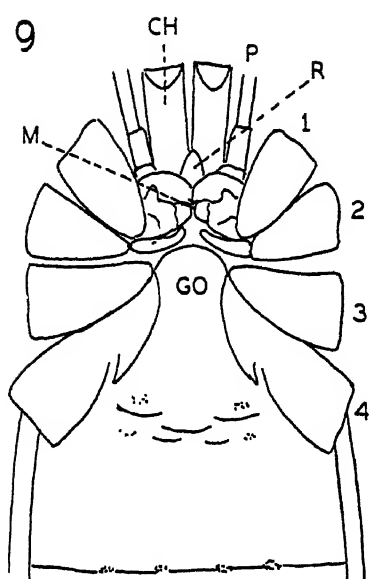


PLATE 4

The coxo-sternal region in Arachnida

FIGURE 13. *Prokopenenia wheeleri* (Rucker), a North American representative of the Order Palpigradi. CH - chelicera. P - pedipalp. 1 - 4 pedal coxae. ST - Sternum 2+3. MST - Metasternum. All coxae are free.

FIGURE 14. *Labochirus proboscideus* (Butler), male, a representative of the Order Thelyphonida from Ceylon. Although the pedipalpal coxae have the appearance of being independent of and merely in contact with each other, they are permanently grown together in the median line and the wall between them is reduced to a ventral, internal crest. All pedal coxae are free. A1 - first abdominal sternite. A2 - second abdominal sternite.

FIGURE 15. *Kustarachne tenuipes* Scudder, a representative of the fossil Order Kustarachnae. The pedipalpal coxae are completely fused with each other, without a trace of the median line.

FIGURE 16. *Trithyreus pentapeltis* Cook, a North American representative of the Order Schizomida. The pedipalpal coxae are fused as in Thelyphonida. The third pedal coxae are contiguous in the median line and practically immobile. The other pedal coxae are free.

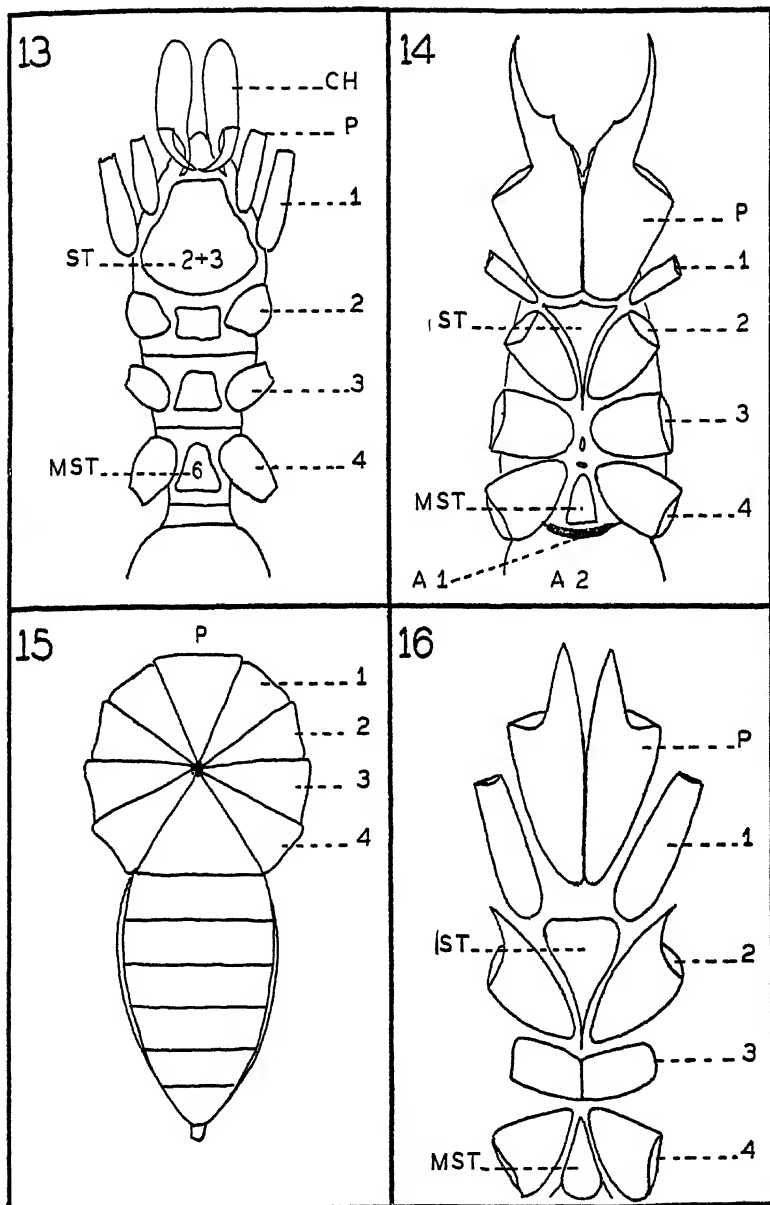


PLATE 5
The coxo-sternal region in Arachnida

FIGURE 17. *Tarantula palmata* (Herbst), from Panama, a representative of the Order Phrynichida. All coxae are movable, without gnathites; the first pedal coxae are small and wedged in between the pedipalpal and second pedal coxae. P - pedipalp. 1 - 4 - pedal coxae. PST - prosternum.

FIGURE 18. *Liphistius malayanus* Abraham, from Fed. Malay States, a representative of the Suborder Liphistiomorphae of the Order Araneae. All coxae movable. CH - chelicera. P - pedipalp. 1 - 4 - pedal coxae. L - lower lip. R - upper lip (rostrum). ST - sternum. MST - metasternum.

FIGURE 19. *Trigonotarbus johnsoni* Pocock, a European representative of the extinct Order Trigonotarbi, new. All coxae are movable.

FIGURE 20. *Pleophrynus ensifer* Petrunkevitch, a North American representative of the extinct Order Trigonotarbi. All coxae are movable. GO - genital opening.

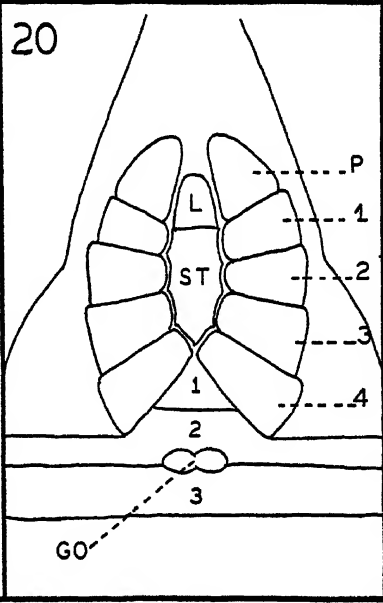
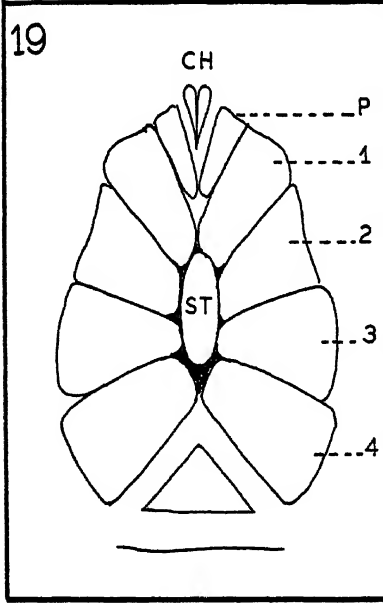
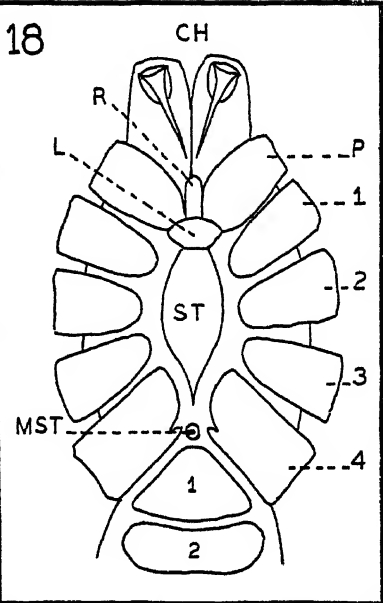
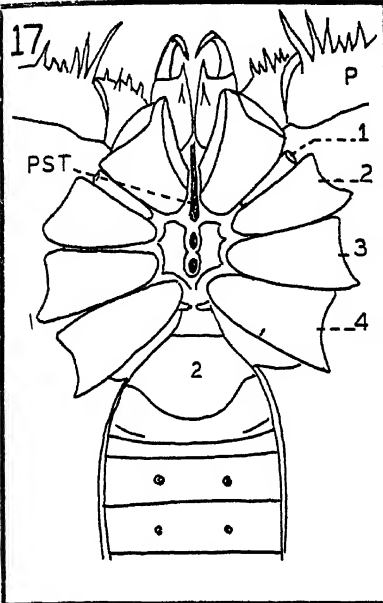


PLATE 6

The coxo-sternal region in Arachnida

FIGURE 21. *Cryptocellus dorotheae* Gertsch, a North American representative of the Family Ricinoididae of the Order Ricinulei. The pedipalpal coxae are fused and immobile. The first pedal coxae are fused with the second of the same side, the second and third not only with each other but also with their mates of the opposite side. Only the fourth pedal coxae are movable. C - cucullus. CH - chelicera. P - pedipalp. 1 - 4 legs (the numerals placed as in the pedipalp in the trochanter). GO - genital opening. L - locking device for fourth coxae.

FIGURE 22. *Curculioides scaber* (Scudder) a North American Palaeozoic representative of the Family *Curculioididae* of the Order Ricinulei.

FIGURE 23. *Polyochera punctulata* Scudder, a North American Palaeozoic representative of the Family *Polyocheridae* of the Order Ricinulei.

FIGURE 24. *Solpuga venator* Pocock, from South Africa, a representative of the Order Solifugae. All coxae are immobile. B - beak formed by the fused upper and lower lips.

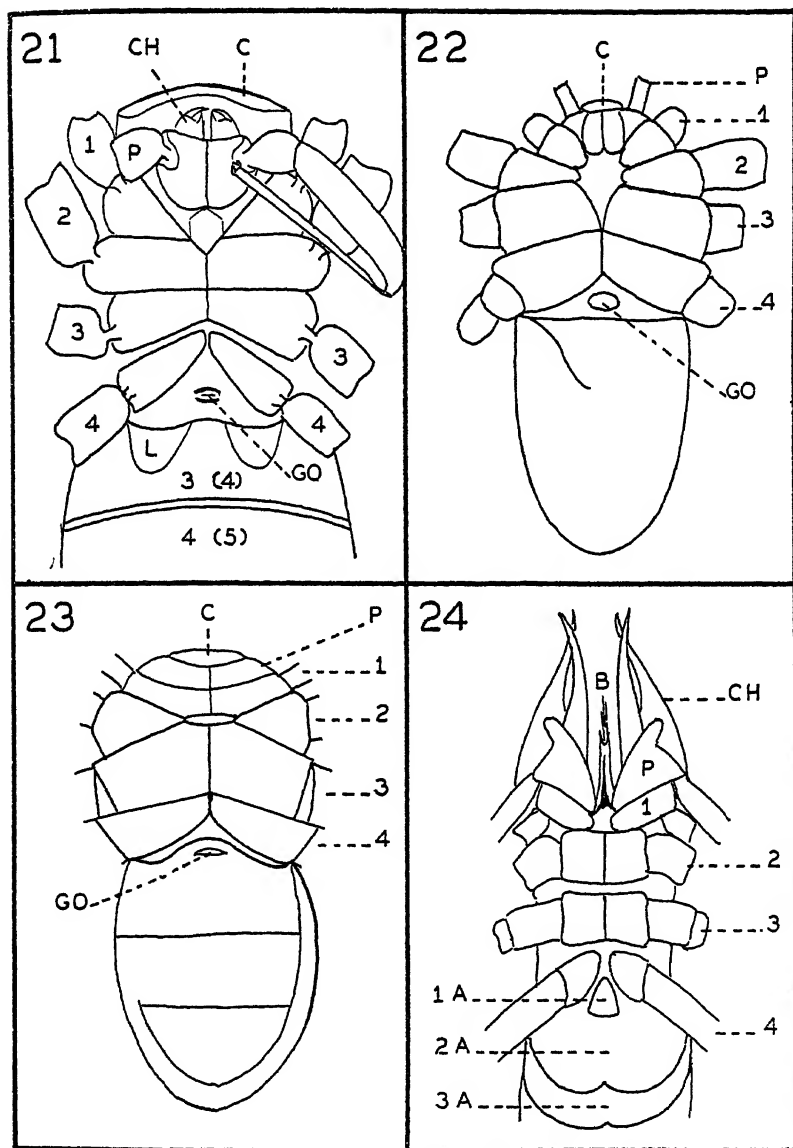


PLATE 7

Inside view of
the coxo-sternal region in Arachnida,
Eurypterida and Xiphosura

FIGURE 25. *Plesiosiro madeleyi* (Pocock), a European representative of the extinct Order Haptopoda. The coxae of the chelicerae are wedged in between those of the pedipalpi, but apparently were somewhat movable. All pedal coxae were movable. CH - chelicerai coxae. P - pedipalpal coxae. 1 - 4 pedal coxae. M - mouth. ST - sternum. 1S - first abdominal sternite.

FIGURE 26. *Cryptomartus priesti* (Pocock), a European representative of the extinct Order Anthracomarti. Movability of coxae similar to that in Haptopoda.

FIGURE 27. A representative of the extinct Class Eurypterida after Størmer. All coxae were free. E - endostome.

FIGURE 28. *Xiphosura (Limulus) polyphemus* (Linnaeus) a North American representative of the Class Xiphosura. All soft tissues have been removed by potassium hydrate. The coxae appear as cavities in the soft ventral sternal wall. CHI - chilaria. E - endostome. Compare with Figure 228.

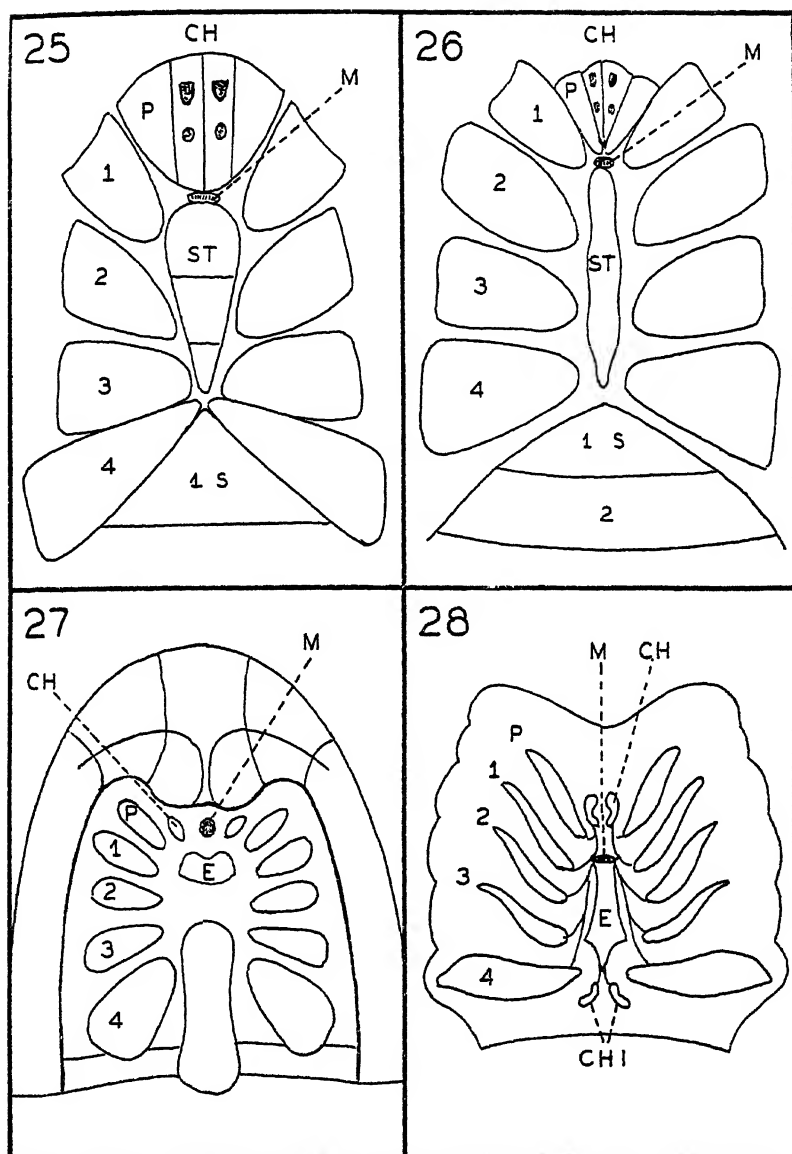


PLATE 8

FIGURE 29. Inside view of the cheliceral and pedipalpal coxae of *Cryptomartus priesti* (Pocock), No. 31237, enlarged ca. x 27. C - partition between the right cheliceral and pedipalpal coxal cavities. CH2 - the second joint of the chelicerae. DO - the cavity at the bottom of the cheliceral coxae, leading into the second cheliceral joint. F - the cavity of the pedipalpal femur. PO - the cavity at the bottom of the cheliceral coxae, leading into the external spur of the coxa. S - the wall between the cavities of the two cheliceral coxae. T - small circular cavities leading into tubercles forming a row on the pedipalpal coxa. Compare with Figure 208.

FIGURE 30. Inside view of the cheliceral and pedipalpal coxae of *Cleptomartus plautus* n.sp., No. 7916, enlarged ca. x 16. The cheliceral coxal cavities appear to be opened much wider than in figure 29. C - the inside surface of the coxal wall of the left chelicera. CH2 - the second joint of the chelicerae. CM - slightly corrugated surface of the inner wall of the carapace superimpressed over the chelicerae. MS - muscle? PTR - protractor of the first right leg. S - wall between the cavities of the cheliceral coxae. PA - cavity of the patella. Compare with Figure 222.

FIGURE 31. Dorsal view of the juncture between the carapace and the abdomen in *Mastigoproctus giganteus* when the first tergite is almost completely hidden under the carapace.

FIGURE 32. Same specimen with the first tergite completely exposed. CM - the connecting membrane.

FIGURE 33. Diagrammatic longitudinal section through the first tergite, showing the bent anterior edge facilitating the overlapping and serving for the attachment of the connecting membrane.

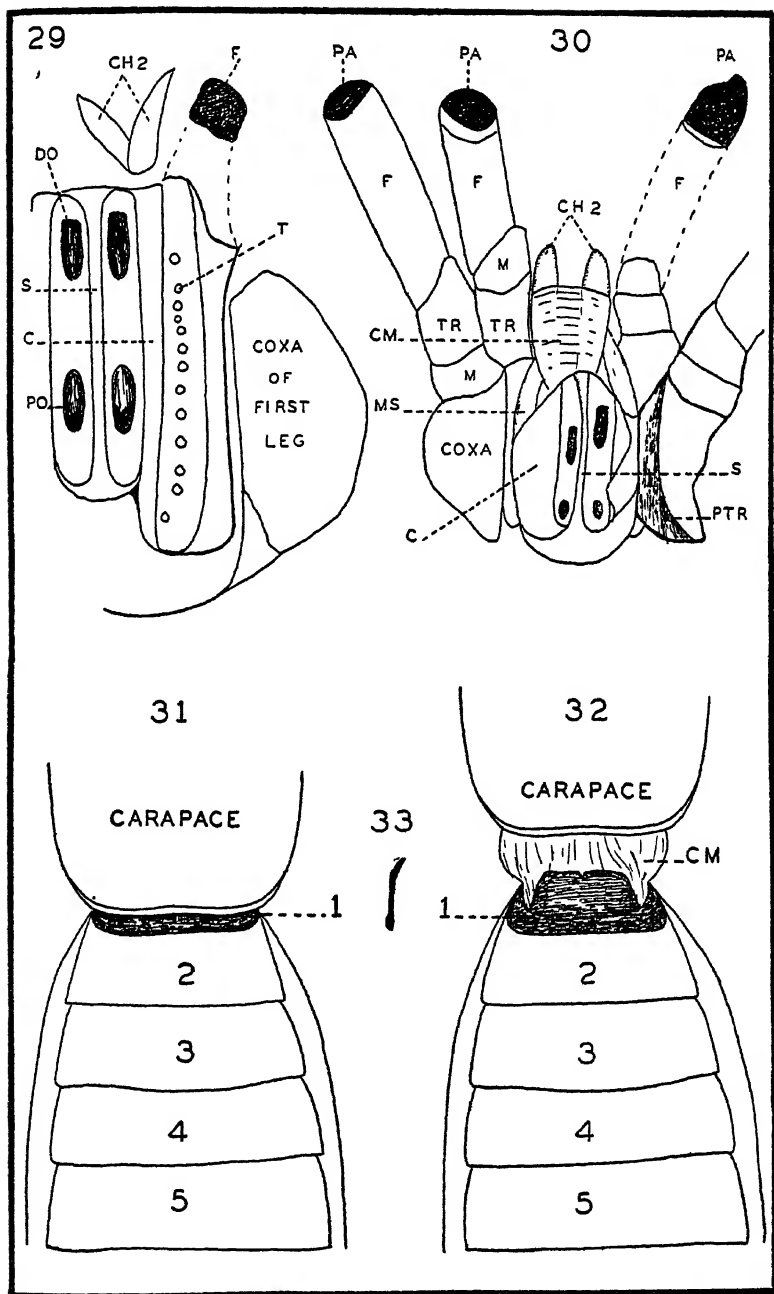


PLATE 9

Relation between dorsal and ventral abdominal lines in *Anthracomarti*

Dorsal lines are shown in red, ventral lines in black.

FIGURE 34. *Cryptomartus hindi* (Pocock), No. 31253. It will be noticed that the dorsal and ventral lines do not coincide and that the two surfaces separate along their lateral edge. Only a portion of the abdomen is shown. $\times 8$.

FIGURE 35. *Cryptomartus priesti* (Pocock), No. 31268, the ventral and dorsal abdominal walls, shown separately in Figures 53 and 54, are superimposed here to show their mutual relationship. $\times 16$.

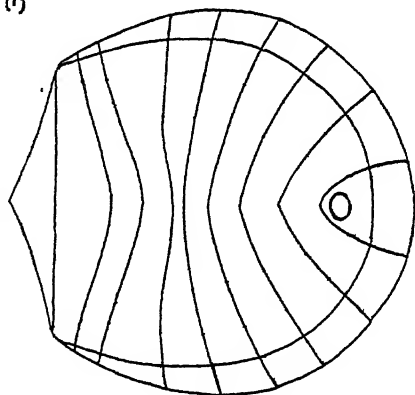
FIGURE 36. Diagrammatic longitudinal section through the tenth tergite of *Cryptomartus hindi*. The dorsal line is considerably longer than the ventral one. $\times 8$.

FIGURE 37. *Cryptomartus hindi* (Pocock), No. 13955. The last two segments of the ventral body wall, $\times 8$. The oval represents the anal operculum.

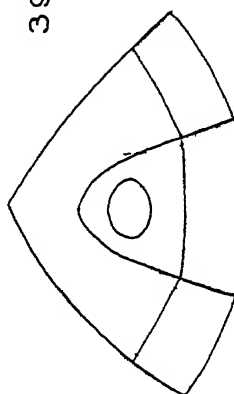
FIGURE 38. The last two segments of the dorsal body wall of the same specimen No. 13955. $\times 8$.

FIGURE 39. The preceeding figure reversed and superimposed over the figure of the ventral wall. $\times 8$.

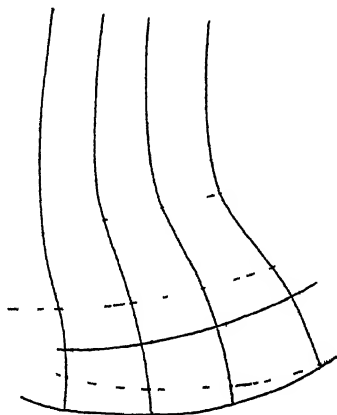
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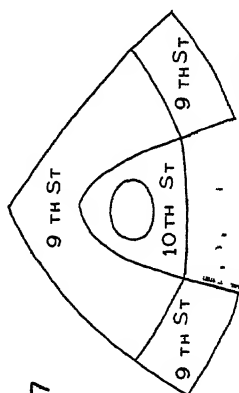
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PLATE 10

FIGURE 40. Connection between the carapace and the abdomen in *Anthracosiro woodwardi* Pocock, No. 1552, x ca.26. C - the edge of the carapace. F - a fissure in the matrix. MEM - connecting membrane. The radiating lines between the carapace and the abdomen are dorsal muscular fibers, plainly visible. Compare with Figure 247.

FIGURE 41. *Cryptomartus priesti* (Pocock), No. 31264. Anterior portion of the dorsal abdominal wall showing the exposed first tergite and the curved strip along its anterior edge, serving for the attachment of the connecting membrane. x 12. Compare with Figure 204.

FIGURE 42. *Cryptomartus hindi* (Pocock), No. 31253. Anterior portion of the dorsal abdominal wall showing the exposed first tergite as in the preceding figure. x 8.

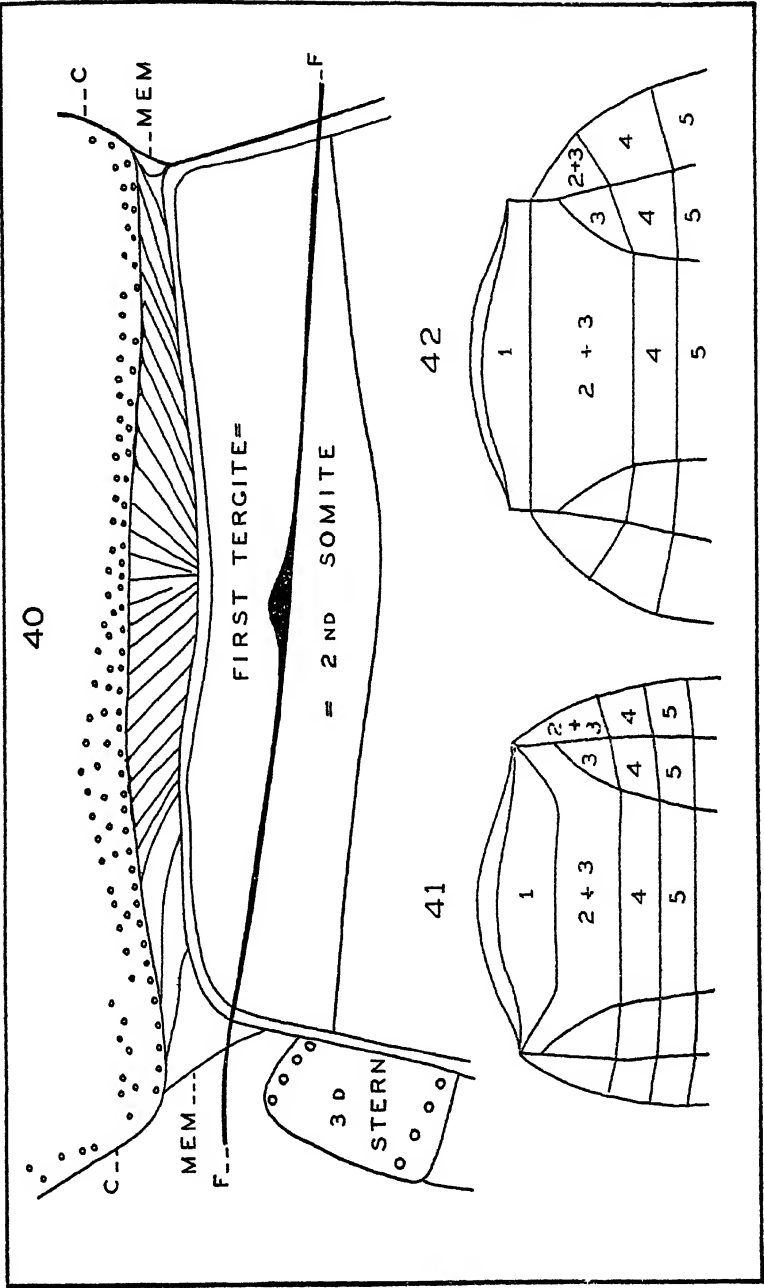


PLATE 11

Mastigoproctus giganteus (Lucas)

a common Recent whip scorpion from Arizona

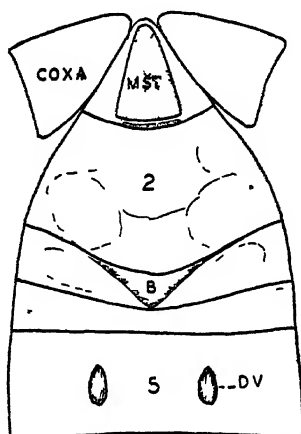
FIGURE 43 Ventral view of the anterior portion of the abdomen of a male, recognizable by the triangular, slightly raised area in the middle of the third sternite. The first sternite is reduced to a narrow strip. The genital opening is not visible externally. It is situated at the posterior edge of the second sternite. MST - metasternite B - the triangular, raised area of the third sternite DV - dorso-ventral muscle

FIGURE 44 Ventral view of the anterior portion of the abdomen of a female, characterized by the triangular, slightly raised area of the second sternite. Notice that the apex of the triangle is directed forward, whereas in the male it is directed backward GO - genital opening

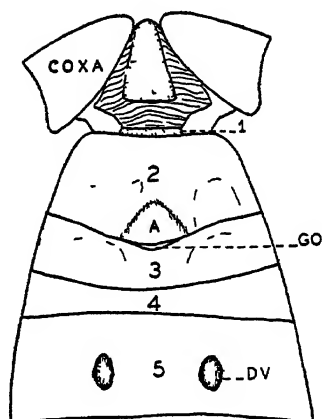
FIGURE 45. Inside view of the male specimen shown in figure 43, after all soft tissues have been removed AP - pulmonary apodeme for the attachment of muscles used in respiration ATR - genital atrium VS - seminal vesicle

FIGURE 46 Inside view of the female specimen shown in Figure 44, after all soft tissues have been removed

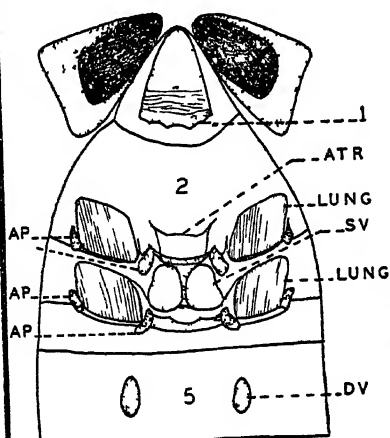
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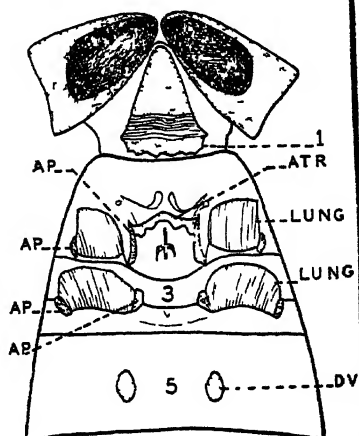


PLATE 12

Cleptomartus plautus n. sp.

FIGURE 47. Inside view of the genital region of a male, No. 18336. x 20.
AP - pulmonary apodeme. A, B and C - successive deep depressions.

FIGURE 48. Inside view of the genital region of a female, No. 7916. x 20.
In both sexes the genital opening is in depression A. It is shown in the insert. The pair of round receptacles are visible.

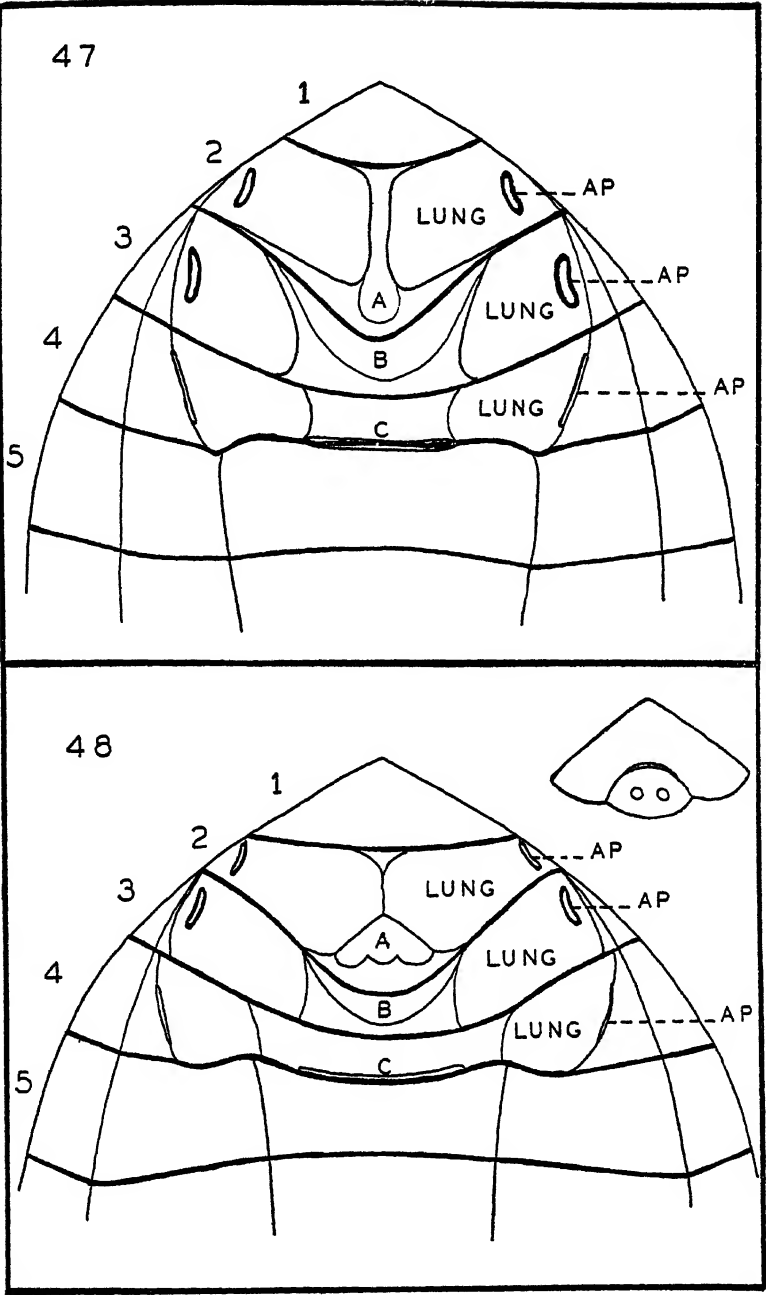


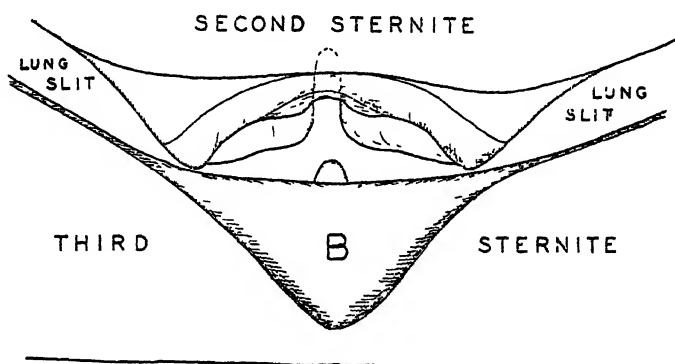
PLATE 13

Mastigoproctus giganteus (Lucas)
a common Recent whip-scorpion from Arizona.

FIGURE 49. The genital opening of a male, viewed from below at a much greater magnification than in figure 43. B - the triangular, raised area characteristic of a male.

FIGURE 50. A microscopic section parallel to the plane of symmetry and close to it, to show the position of the mouth and camarostome. CAM - camarostome (space between the upper lip and the lower lip, the latter forming in Thelyphonida part of the inner walls of the fused pedipalpal coxae). CO - Dorsal opening of the camarostome. It has more or less the shape of a parabola. DO - opening of distal sensory pouch. PO - proximal sensory area. CR - median crest representing the last remnant of the fused inner wall of the pedipalpal coxae. M - mouth. DPH - dilating muscles of the pharynx, PH.

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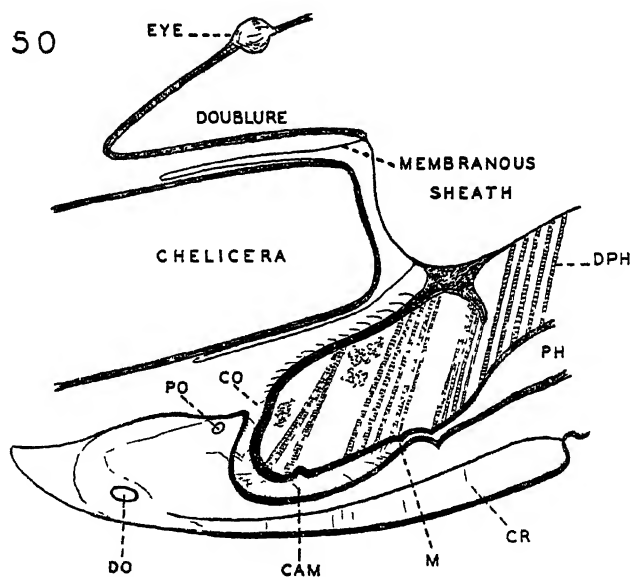


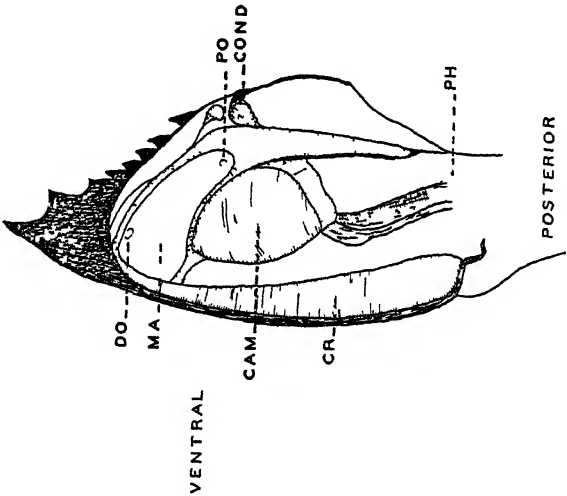
PLATE 14

Mastigoproctus giganteus (Lucas) a common Recent whip scorpion from Arizona

FIGURE 51 View of the left pedipalpal coxa after the left wall has been removed and all soft tissues dissolved in KOH DO - opening of the distal sensory pouch MA space occupied by various tissues, now removed PO - proximal sensory area CAM - camarostome Only the lower wall of it is visible, formed by the inner walls of the fused pedipalpal coxae It has the shape of a bowl CON condyle for the articulation of the trochanter CR median crest representing the last remnant of the fused median walls of the pedipalpal coxae PH - pharynx

FIGURE 52 View from above of the pedipalpal coxae and of the camarostome after the removal of the carapace and of the chelicerae CO - dorsal opening of the camarostome, having the shape of a parabola and extending to the base of the upper lip LM ES - esophagus SC - scopula of short hair on the soft, membranous area in which the sensory pouches DO and PO are situated

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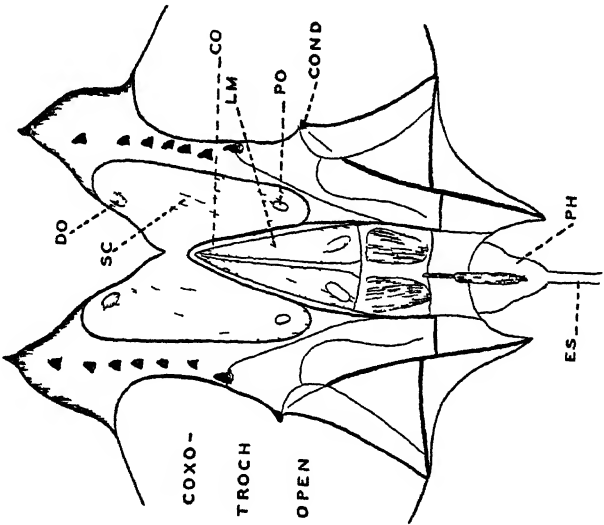


PLATE 15

Segmentation of the abdomen in Anthracomarti

FIGURE 53. *Cryptomartus priesti* (Pocock), No. 31268, x 16. Dorsal surface.

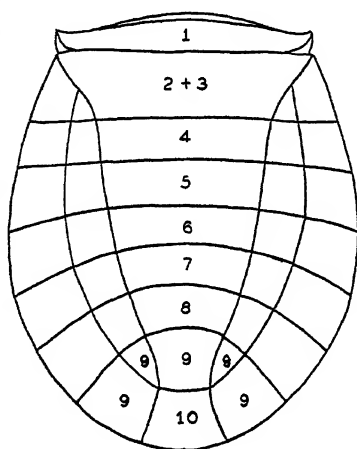
FIGURE 54. Same specimen, ventral surface. The two figures are shown superimposed in figure 35. A - anus.

FIGURE 55. *Anthracomartus völkelianus* Karsch, enlarged copy of Karsch's Figure 1, slightly corrected for symmetry and with the numbering of the tergites brought to conform with all other representatives of the Order. A photographic reproduction of Karsch's figure is given in Figure 192.

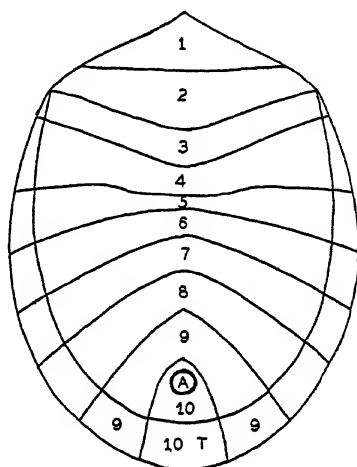
FIGURE 56. *Promygale bohémica* Fritsch. A reconstruction of its segmentation on the basis of Fritsch's Figure 1 on Plate 15, but with following modifications: The parallel line across the ninth tergite, shown in the original, is omitted as it belongs to the ventral surface. The eyes are omitted as their existence is very doubtful. Only one leg drawn completely for reasons of space.

FIGURE 57. *Anthracophrynus tuberculatus* Andrée. Suggested reconstruction on the basis of his figure. What he supposed to be portion of the carapace is interpreted here as portion of the abdominal tergites 1 and 2 + 3.

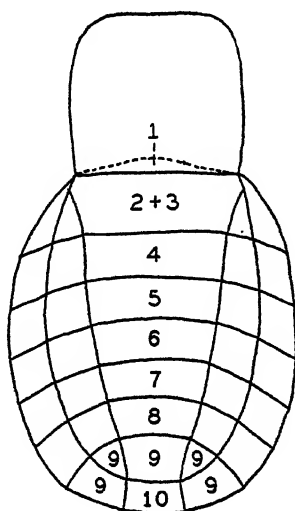
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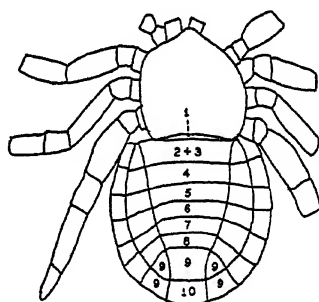
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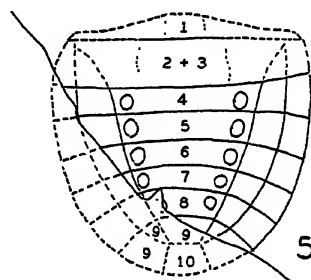


PLATE 16

Segmentation of the abdomen in Anthracomarti

FIGURE 58. *Pleomartus trilobitus* (Scudder). Cotype, USNM No. 1753d (37982), x 8. This drawing was made after reexamination of the specimen, a photograph of which is shown in Figure 190.

FIGURE 59. *Coryphomartus triangularis* (Petrunkévitch). Type, USNM No. 37968. x 5.5. This drawing was made after reexamination of the specimen and incorporates new features. A photograph of the specimen is shown in Figure 191.

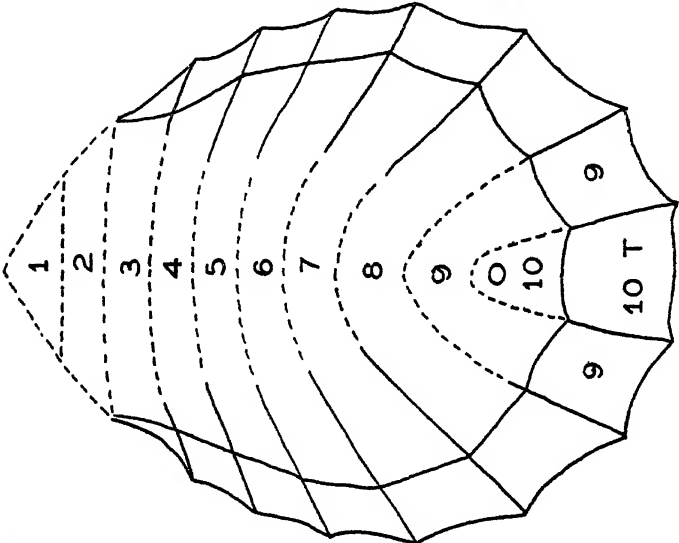
PLATE 17

Segmentation of the abdomen in *Anthracomarti*
Brachypyge carbonis Woodward

FIGURE 60. Reconstruction of the dorsal surface on the basis of Woodward's original figure and Pruvost's photograph and drawings. Pruvost shows ventral lines on the dorsal surface. They are omitted in our reconstruction.

FIGURE 61. Reconstruction of the ventral surface on the same basis.

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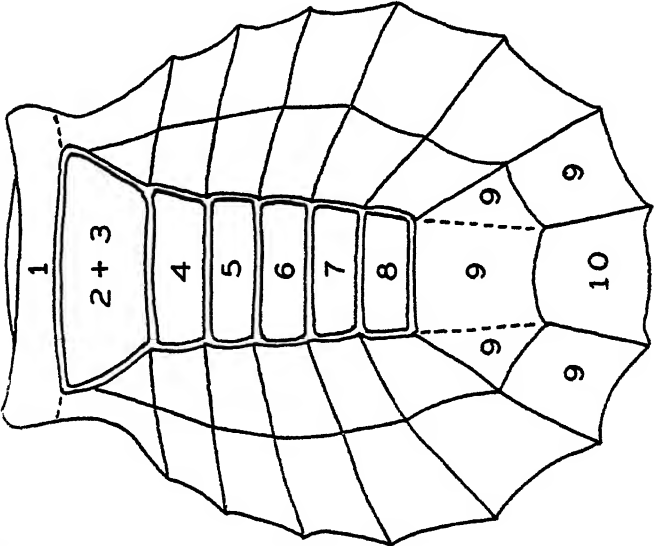


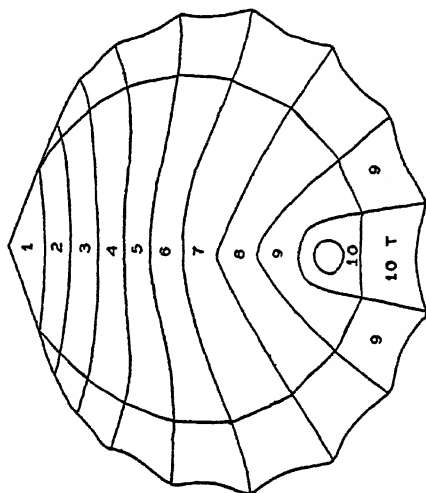
PLATE 18

Segmentation of the abdomen in *Anthracomarti*
Majocercus carbonis (Howard and Thomas)

FIGURE 62. Reconstruction of the dorsal surface on the basis of Pruvost's figure, but with omission of ventral lines and with the numbering of the tergites changed to conform with all other *Anthracomarti*.

FIGURE 63. Reconstruction of the ventral surface of the same specimen on the same basis as in the preceding figure.

63



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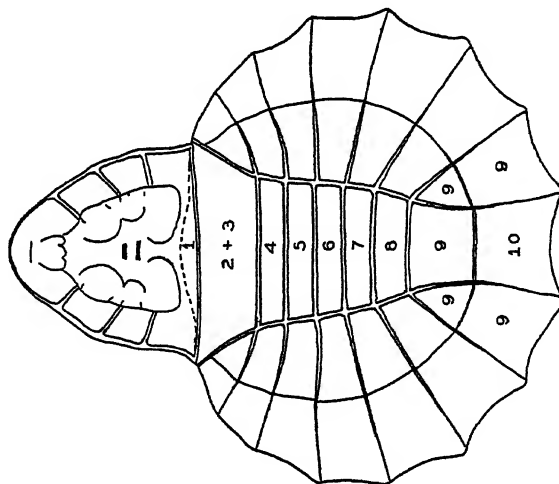


PLATE 19

Segmentation of the abdomen in *Anthracomarti*

FIGURE 64. *Cryptomartus hindi* (Pocock). Dorsal surface of Pocock's Paratype No. 13955 after cleaning, x 6.5.

64

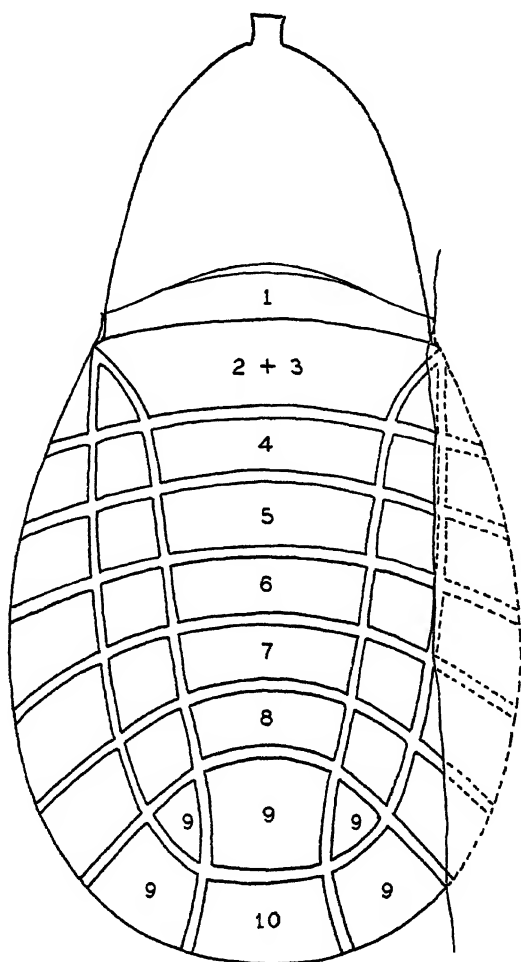


PLATE 20

Segmentation of the abdomen in *Anthracomarti*

FIGURE 65. *Cryptomartus hindi* (Pocock). Ventral surface of Pocock's Paratype No. 13955 after cleaning. x 6.5.

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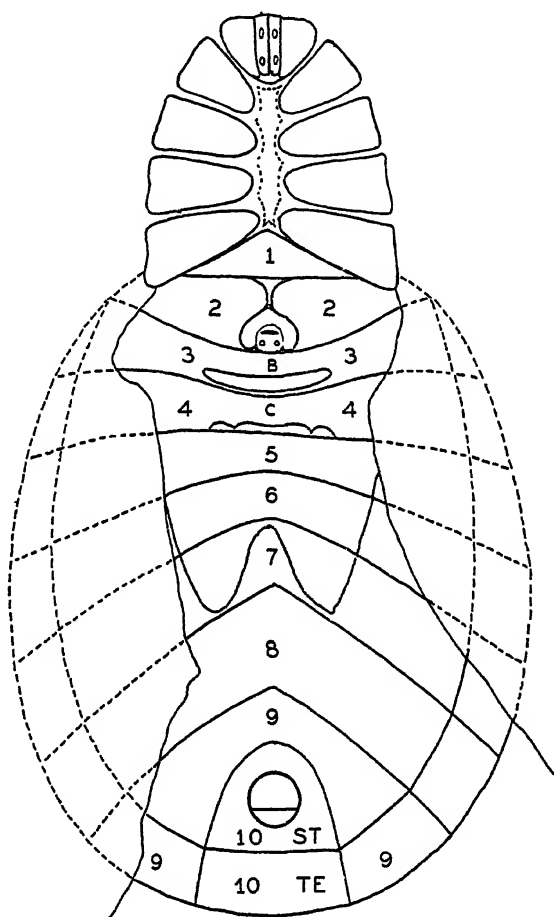
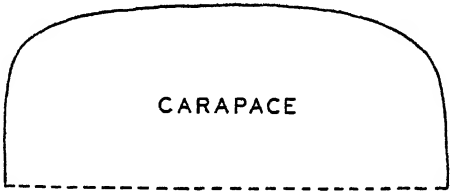


PLATE 21

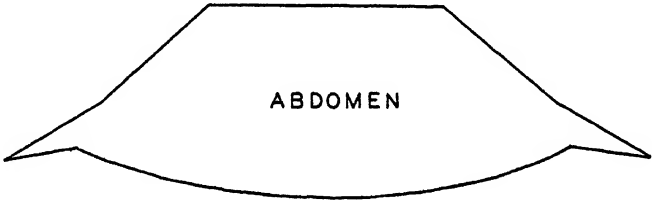
FIGURE 66. A series of diagrammatic transverse sections through the cephalothorax and the abdomen of species of *Cryptomartus* and *Cleptomartus*. The sections were made through plastic clay casts. The straight dotted lines represent the horizontal plane passing through the ventral edges of the carapace. CR - *Cryptomartus*. CL - *Cleptomartus*. The same magnification of x 12 is used in all sections.

66



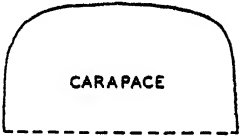
CARAPACE

CR. HINDI



ABDOMEN

CR. PRIESTI



CARAPACE



ABDOMEN

CL. PLANUS



CARAPACE



ABDOMEN

CL. PLAUTUS



CARAPACE



ABDOMEN

PLATE 22

Cryptomartus hindi (Pocock)

FIGURE 67. The crest of specimen No. 13955 (Pocock's Paratype), viewed from the inside after cleaning and removal of extraneous matter. x 24.

FIGURE 68. The anal operculum of specimen No. 13910. x 45. Notice that the anterior valve is much larger than the posterior one.

FIGURE 69. First left leg of specimen No. 18338. x 24. Notice that the metatarsus is shorter than the tarsus.

FIGURE 70. The claw of the first tarsus shown in the preceding figure, enlarged x 85. The claw is on a distinct onychium and above it six pointed bristles are visible.

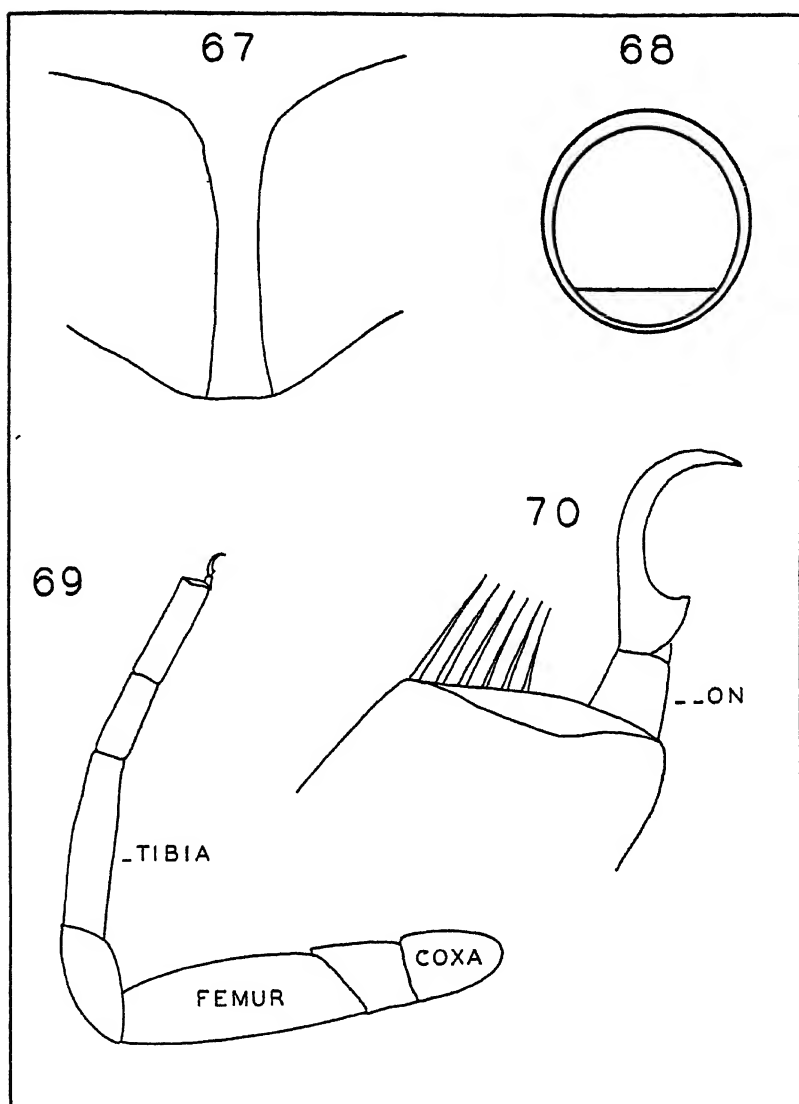


PLATE 23

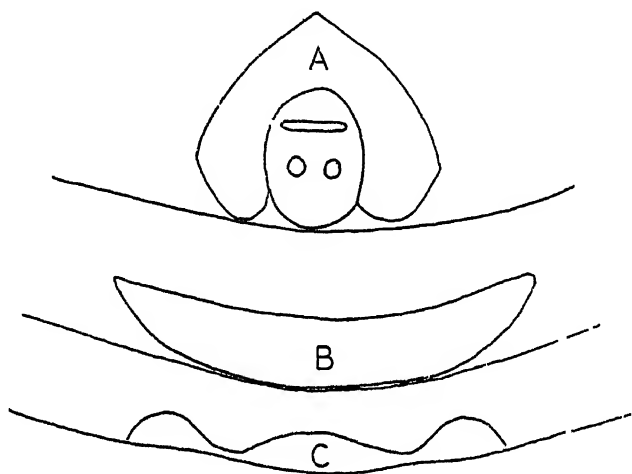
The genital region in *Cryptomartus*

FIGURE 71 *Cryptomartus hindi* (Pocock), No 13955, presumably a female x 22 Depression A is on the second sternite Below the transverse, slit-like genital opening a pair of round openings are visible Presumably they belong to seminal receptacles Depression B is on the third sternite, depression C on the fourth sternite

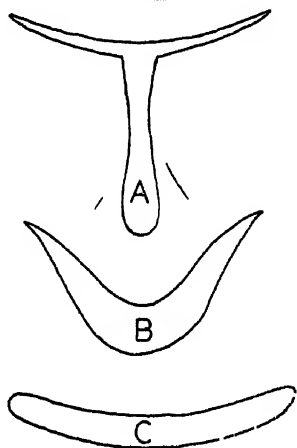
FIGURE 72 *Cryptomartus priesti* (Pocock), No 32837, presumably a male x 10

FIGURE 73 *Cryptomartus priesti* (Pocock), No 15858, presumably a female x 10

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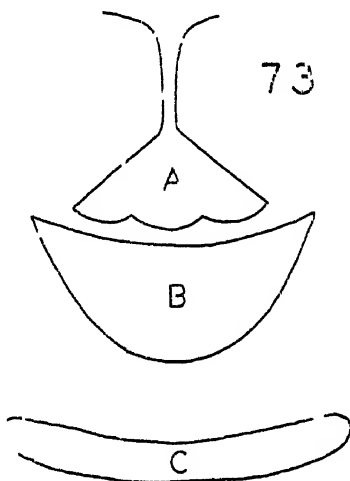


PLATE 24

Cryptomartus priesti (Pocock)

FIGURE 74. Specimen No. 7893, presumably a male. x 7.

FIGURE 75. Fourth right leg of specimen No. 22842, presumably a male.
x 44. Two claws are visible at the end of the tarsus, but an onychium seems
to be wanting.

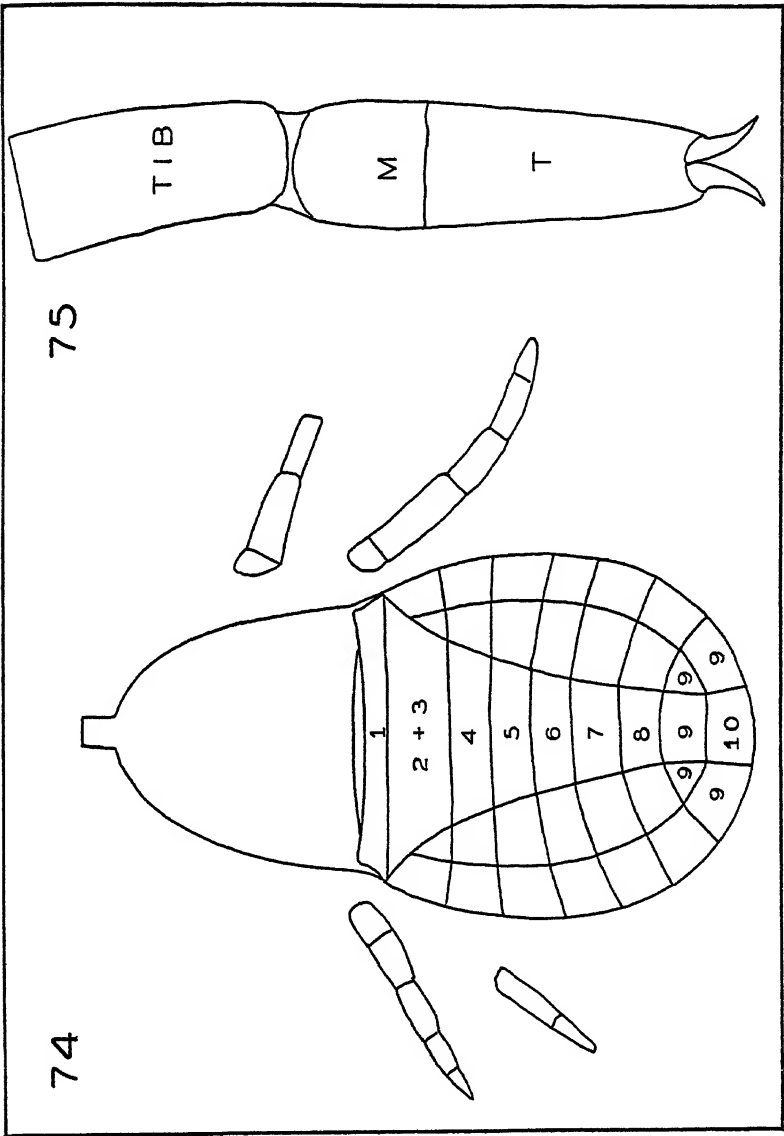


PLATE 25

Cryptomartus priesti (Pocock)

FIGURE 76. Ventral view of specimen No. 31268, presumably a female.
x 7. Between the pedipalpal coxae the coxae of the chelicerae are plainly visible.

76

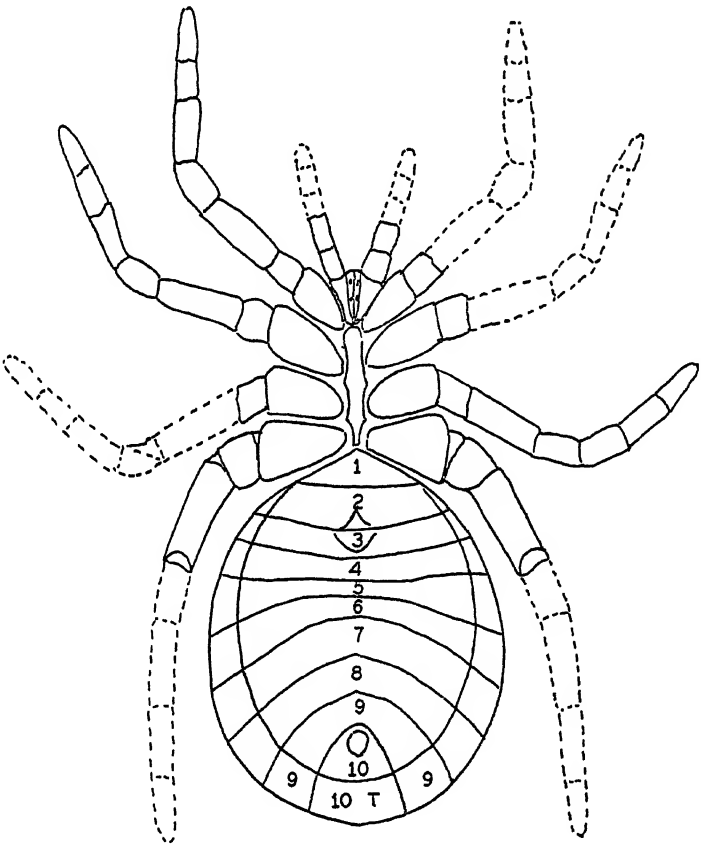


PLATE 26

Cryptomartus priesti (Pocock)

FIGURE 77. The crest of No. 7893, viewed from the inside after cleaning and removal of extraneous matter. x 22.

FIGURE 78. The second joints of the chelicerae of specimen No. 7893. x 44, viewed from in front.

FIGURE 79. The left second joint of the chelicera of specimen No. 7893, viewed in profile. x 44.

FIGURE 80. The third right leg of specimen No. 22842. x 14. The claws are not preserved. Notice that the metatarsus is much shorter than the tarsus.

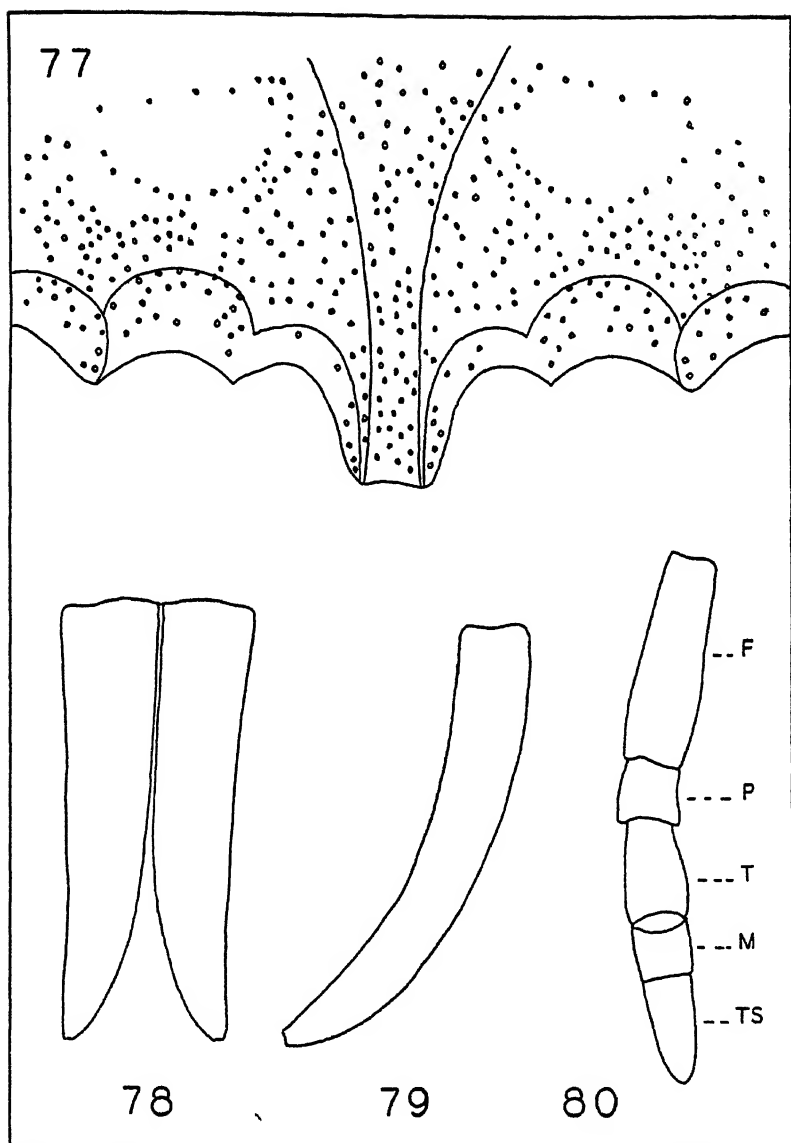


PLATE 27

Cleptomartus plautus n. g., n. sp.

FIGURE 81. Dorsal view of the type specimen No. 15896, x 7. The first abdominal tergite is visible under the carapace and is indicated by the dotted line. There is another transverse depression across the middle of the carapace, which is simply an artificial distortion and is omitted from this drawing. It is visible in the photograph, in Figure 216.

FIGURE 82. The third right tarsus of specimen No. 15896, x 35. There seems to be a little onychium present.

FIGURE 83. The square foramen leading into the patella of the right palp of specimen No. 15896, x 7. The foramen is at the end of the interarticular membrane which is clearly wrinkled in the specimen.

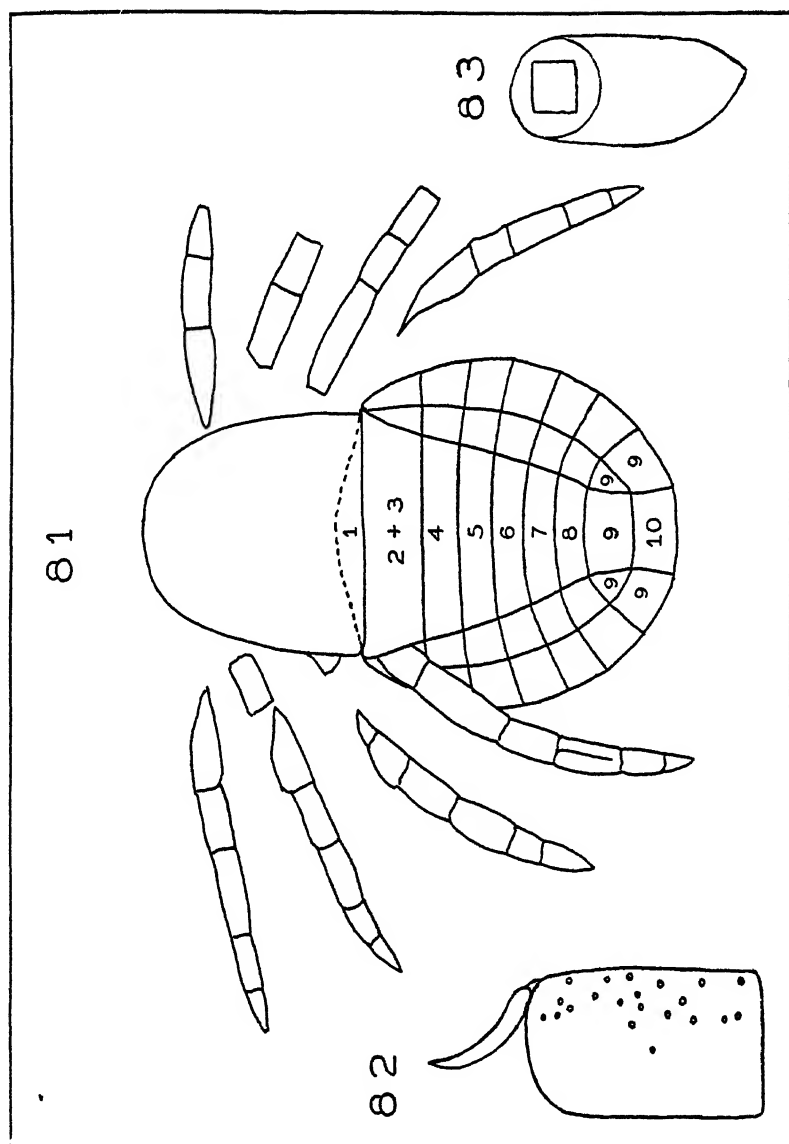


PLATE 28

Cleptomartus plautus n. sp.

FIGURE 84. Profile view of second joint of the right chelicera of specimen No. 15896, x 44.

FIGURE 85. Front view of second joints of the chelicerae of specimen No. 15896, x 44.

FIGURE 86. Profile view of the coxa and second joint of the right chelicera of specimen No. 13956, x 44. MS - the median septum representing the fused mesial walls of the coxae.

FIGURE 87. The genital region of specimen No. 15857. Androtype. x 22. The three depressions—A, B and C.

FIGURE 88. The genital region of specimen No. 7916, a female, x 22.

FIGURE 89. Ventral surface of abdomen of the type specimen No. 15896, x 7.

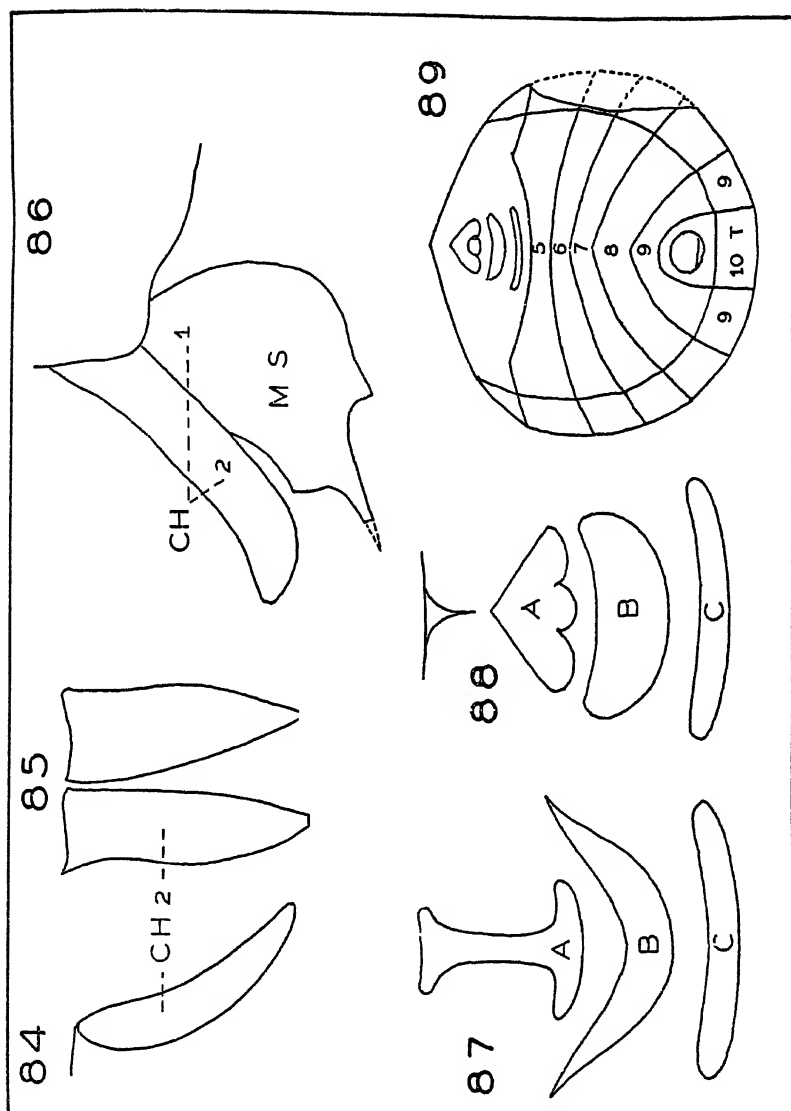


PLATE 29

Cleptomartus planus n. sp. Type specimen No. 7918

FIGURE 90. Dorsal view. The first tergite is not visible. x 7. Piece *a*.

FIGURE 91. Ventral surface partly exposed in the posterior region of the abdomen. x 7. Piece *b*.

FIGURE 92. The anal operculum. x 44. Notice that the anterior valve is much larger than the posterior one.

FIGURE 93. The second joints of the chelicerae viewed from in front. x 44

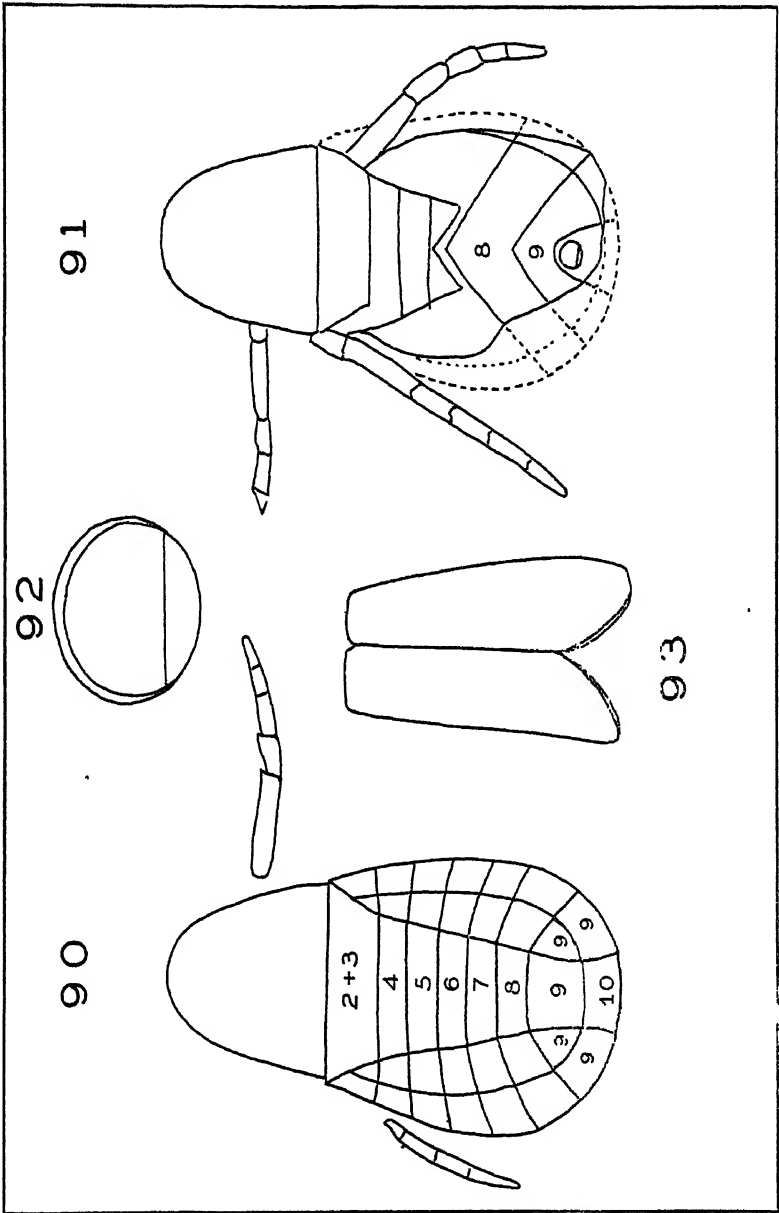


PLATE 30

FIGURE 94. *Plesiosiro madeleyi* Pocock, reconstruction of the ventral surface, based on new evidence furnished by specimen No. 7922. x 5 approximately.

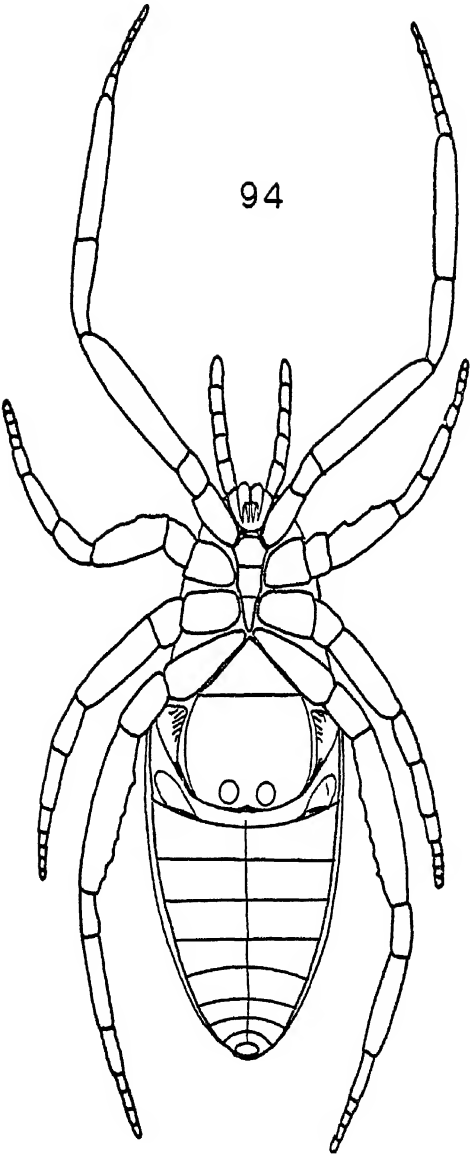


PLATE 31

FIGURE 95. *Plesiosiro madeleyi* Pocock. Dorsal view of specimen No. 7922, x 7. M - metatarsus. The tarsus of the second leg is incomplete. It should have four joints.

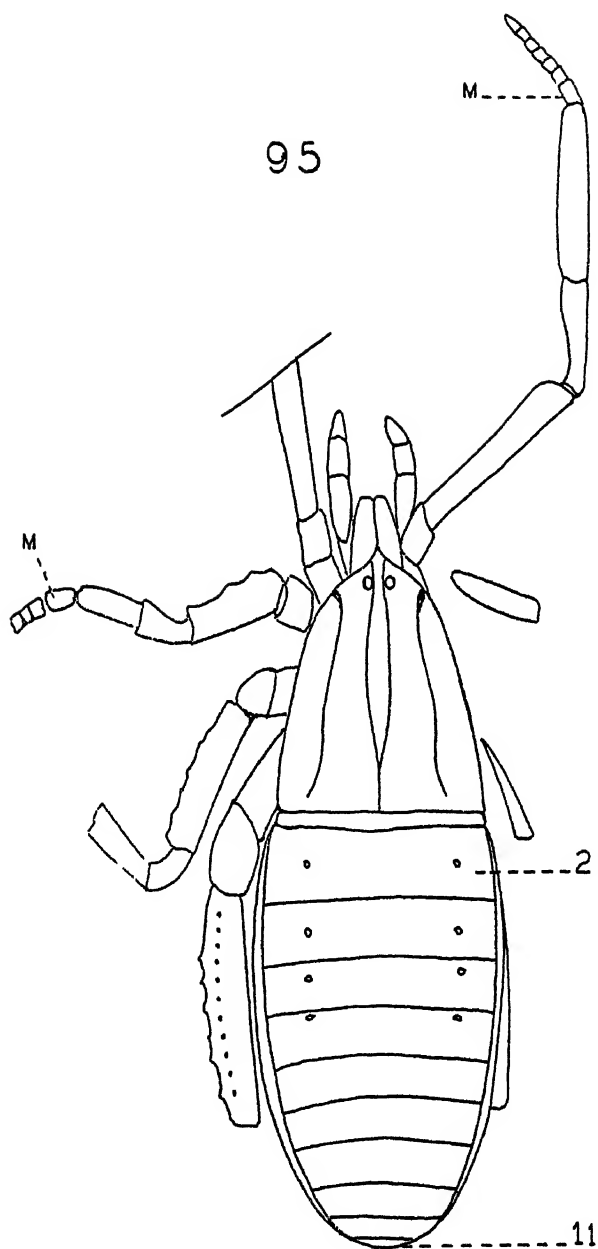


PLATE 32

Plesiosiro madeleyi Pocock, specimen No. 7922

FIGURES 96-99. Metatarsus and tarsus of the four legs. In the fourth leg the terminal (fourth) tarsal joint is distorted and superimpressed over the third joint. x 32.

FIGURE 100. Chelicerae x 3.2.

FIGURE 101. The two lungs of the left side. x 26. The black lines on the lung covers are corrugations of a darker color.

FIGURE 102. The eyes x 67.

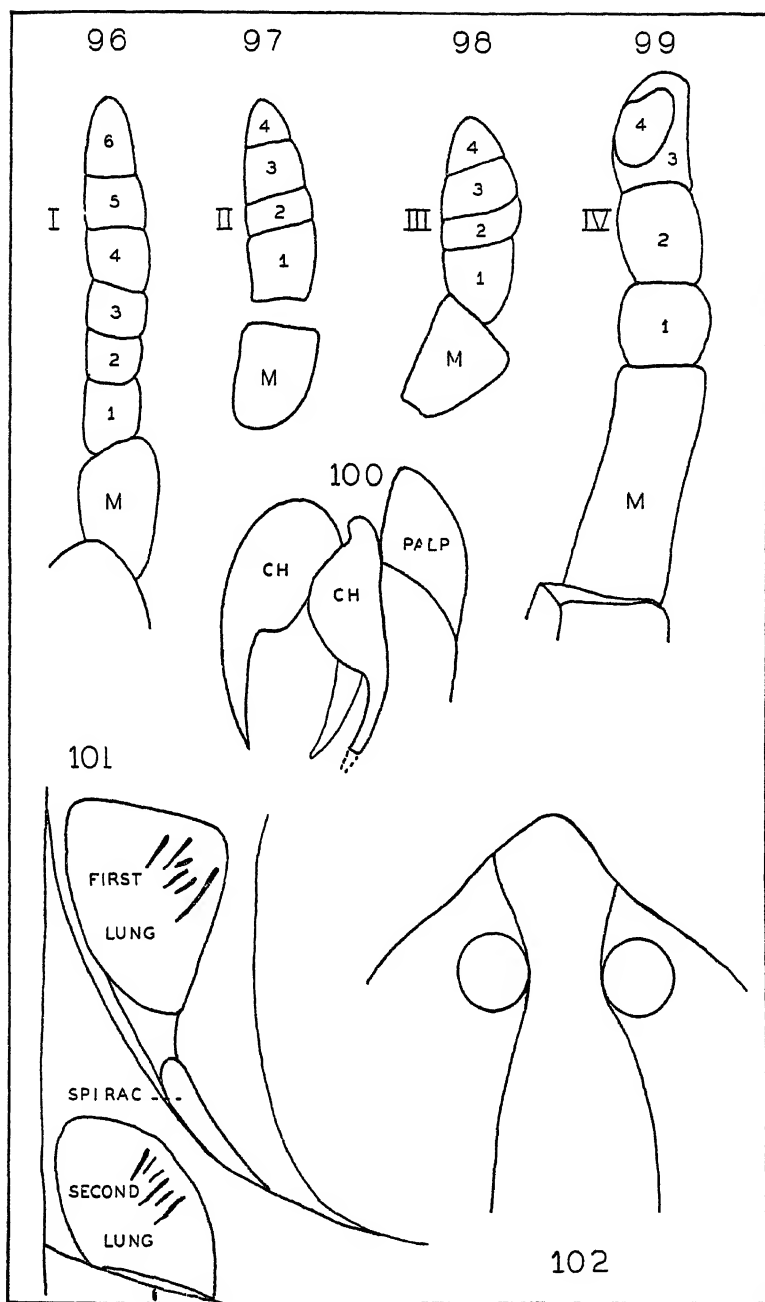


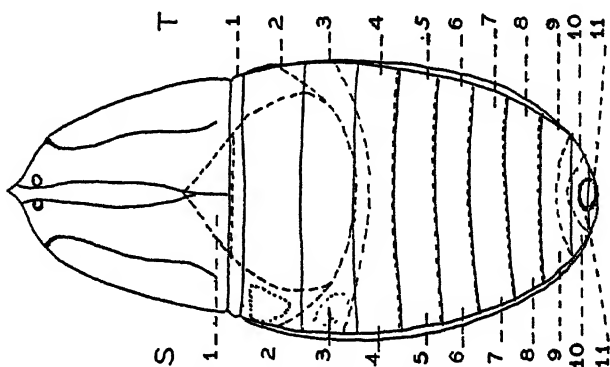
PLATE 33

FIGURE 103. *Plesiosiro madeleyi* Pocock, specimen No. 7922. The two surfaces superimposed to show segmentation. $\times 7$. S - sternites represented by dotted lines. T - tergites shown by solid lines. Notice that all eleven segments have a tergite and a sternite, but only those of the fifth to eighth segments coincide completely. Notice also the extraordinary development of the second sternite. The lungs are shown only on the left side.

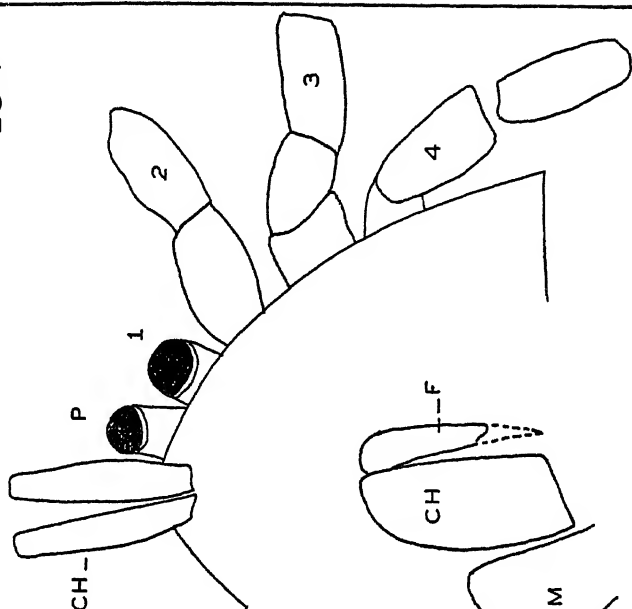
FIGURE 104. *Trigonotarbus johnsoni* Pocock. The right side of the carapace of specimen No. 15859, $\times 20$. CH - chelicera. P - pedipalp.

FIGURE 105. *Trigonotarbus johnsoni* Pocock, No. 15859, ventral piece. Lateral view of chelicerae with fang, $\times 20$.

103



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105

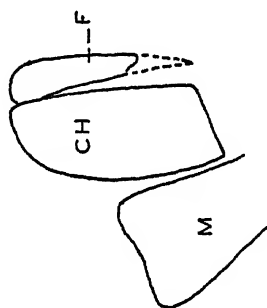


PLATE 34

Trigonotarbus johnsoni Pocock

FIGURE 106. Dorsal view of specimen No. 15897, x 12.

FIGURE 107. End of carapace and eye tubercle with eyes, x 45, specimen No. 31240.

FIGURE 108. Specimen No. 31240, genital region x 85.

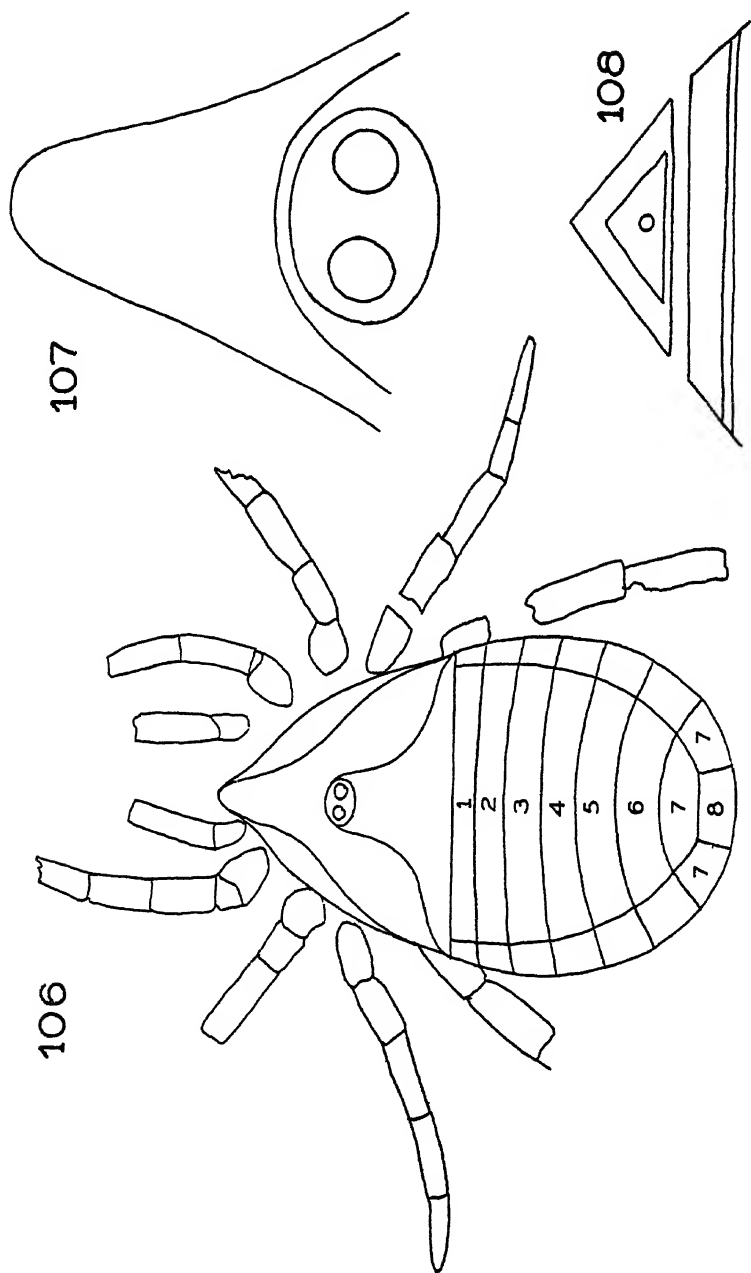


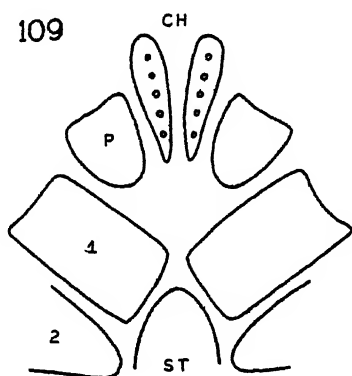
PLATE 35

FIGURE 109. *Trigonotarbus johnsoni* Pocock, specimen No. 31241, anterior portion of the coxo-sternal region, x 45.

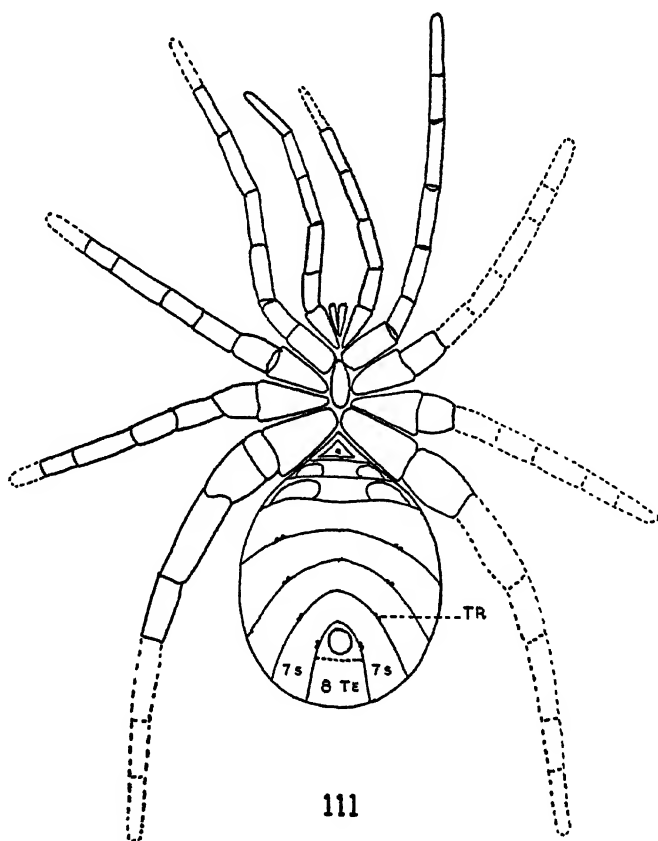
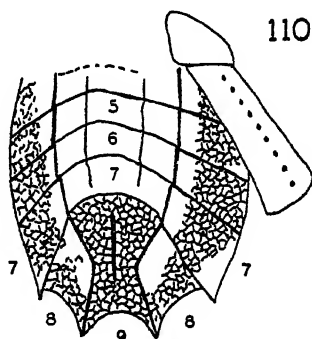
FIGURE 110. *Eophrynus varius* n. sp. Type. In. 39767, x 2.5.

FIGURE 111. *Trigonotarbus johnsoni* Pocock, reconstruction of ventral surface. x 9. TR - paired tubercle, possibly representing tracheal tubes.

109



110



111

PLATE 36

FIGURE 112. *Anthracosiro woodwardi* Pocock. Reconstruction of the dorsal surface on the basis of specimen No. 1552. The missing legs are figured as mirror images of the preserved ones of the opposite side so as to give a better idea of the true appearance of the species. All proportions are true to nature and nothing is added that has no counterpart in the specimen. The figure was made on a much larger scale under binocular microscope and then reduced photographically to its present size which is $\times 5\frac{1}{3}$ times larger than the actual specimen.

112

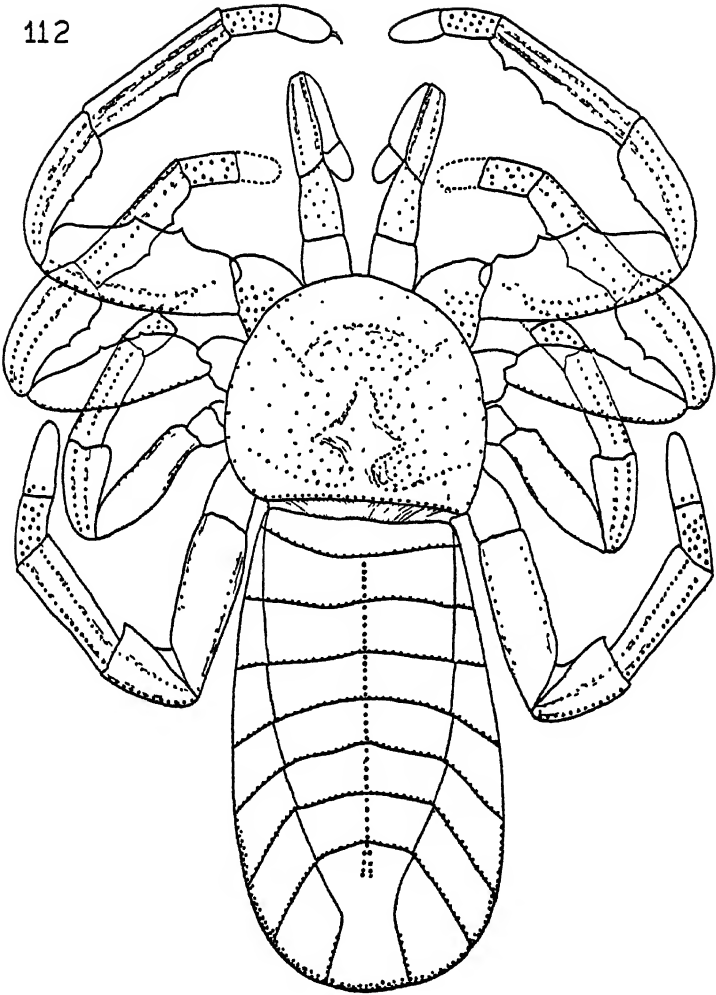


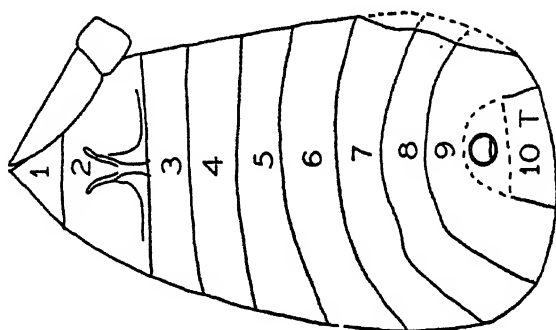
PLATE 37

Anthracosiro woodwardi Pocock

FIGURE 113. Pocock's Paratype No. 1554, dorsal surface viewed from above. The dotted line between tergites 9 and 10 is introduced to indicate that the last visible tergite is composed of two fused ones. In the specimen it is not present. $\times 5.5$.

FIGURE 114. The ventral surface of the same specimen. Compare with Figure 113 and notice that the first *visible* tergite is in reality the tergite of the second abdominal segment and that the first segment has lost its tergite and is represented only by the first sternite. $\times 5.5$.

114



113

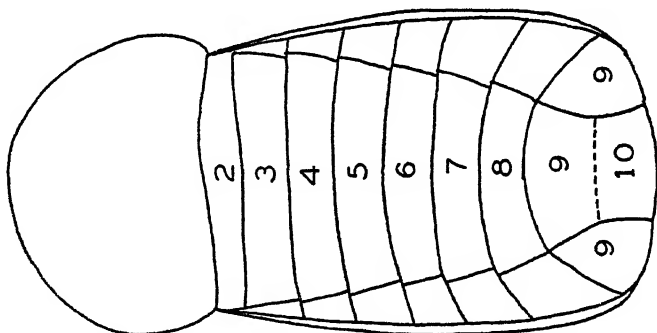


PLATE 38

Anthracosiro woodwardi Pocock

FIGURE 115. The coxo-sternal region of Pocock's Paratype, No. 1554, after cleaning. x 12.

FIGURE 116. Metatarsus and tarsus of first right leg of specimen No. 1552, x 12.

FIGURE 117. Second left leg of specimen No. 1552, x 12, showing arrangement of granules on patella and tibia in two rows and on metatarsus scattered irregularly.

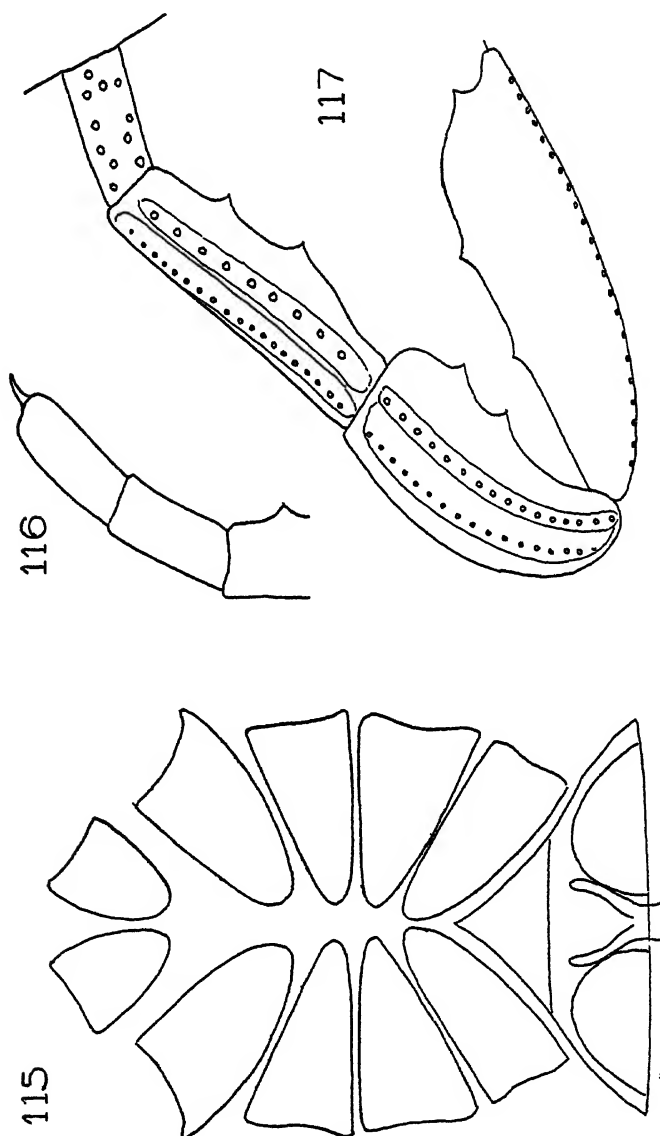


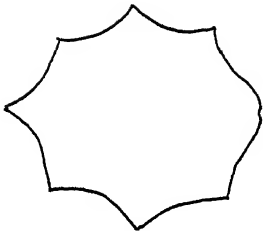
PLATE 39

FIGURE 118 *Palaeocharinoides hornei* Hirst Photographic copy of Hirst's Plate XII, slightly reduced The figure shows the ventral surface superimposed over the dorsal surface in the same piece The numeral 11 is introduced by the author of the present article to conform with Hirst's interpretation The carapace is shown in profile (a) and in front view (b) It has almost the same shape as the carapace of *Cryptomartia hindi* and *C. priesti* and has a similar crest

FIGURE 119 Enlarged figure of the sternum of *Palaeocharinoides hornei*

FIGURE 120 Enlarged figure of the sternum of *Palaeocharinus rhyniensis* Hirst, made from Hirst's figure c on Plate XVI

119



120

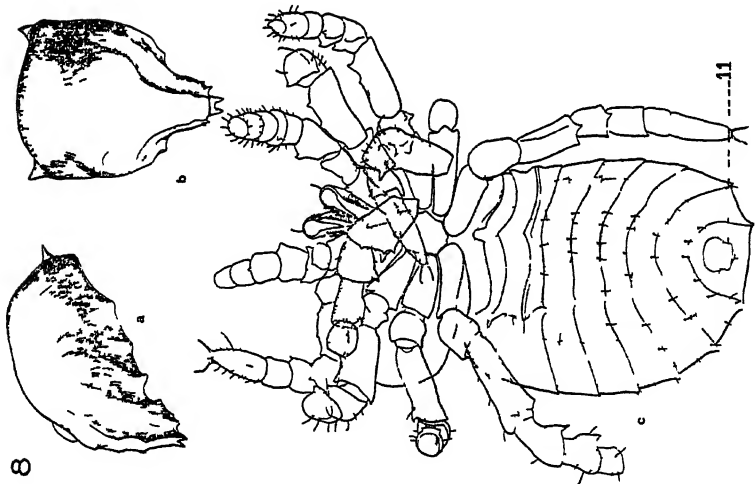
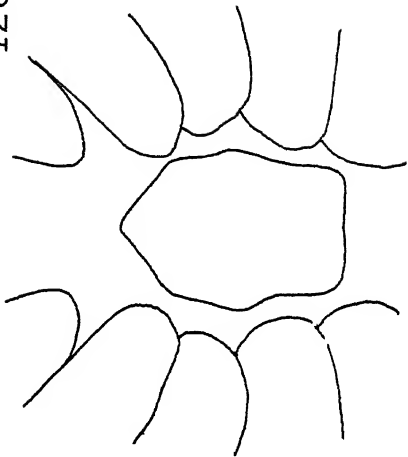


PLATE 40

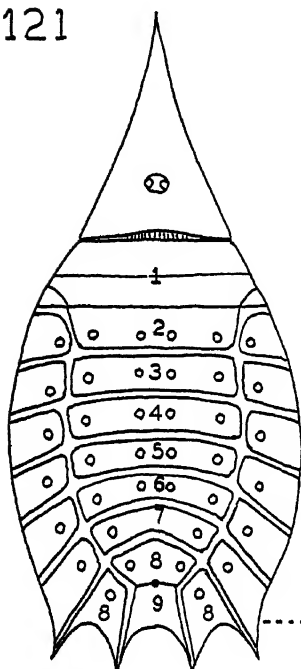
FIGURE 121. *Pleophrynus ensifer* Pentrunkevitch, Type, dorsal surface. NB. This is the same figure as Text-figure 25 in my Palaeozoic Arachnida of Illinois, corrected for symmetry and with the numbering of the tergites fully accounted for. As explained in the text my Text-figure 30 on page 59 of the same paper contains a lamentable and unexplainable error and is, therefore, to be discarded and substituted by the present one. Compare with Figure 259.

FIGURE 122. *Eophrynus prestvicii* (Buckland). A copy of Pocock's figure, slightly enlarged to make it of the same size with the preceding one. The copy was made photographically, then the legs were blocked out and the numbering of the tergites changed to conform with that accepted in the present paper. It will be noticed that the first tergite is subdivided in both *Eophrynus* and *Pleophrynus*, while the ninth tergite is fused with the eighth only in the former.

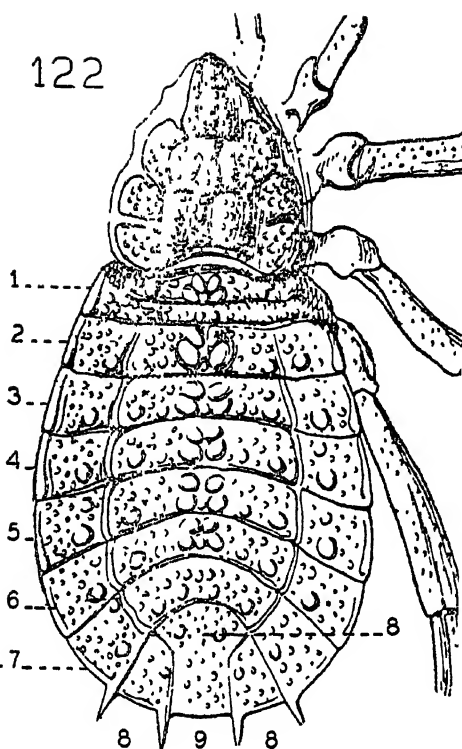
FIGURE 123. *Areomartus ovatus* Petrunkevitch. Type.

FIGURE 124. *Kreischeria verrucosa* Pocock. Photographic copy of Pocock's Figure 40, slightly reduced.

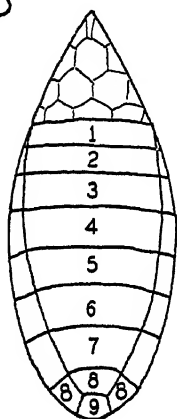
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123



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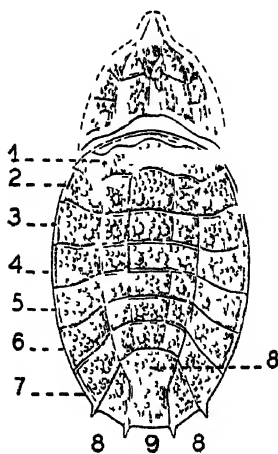


PLATE 41

FIGURE 125. *Trigonomartus pustulatus* (Scudder). A photographic copy of A. P.'s figure 60 on page 103 of the Monograph of Palaeozoic Arachnida of North America, 1913. The numerals indicating the tergites are introduced here, as in the other figures on this plate, to facilitate comparison.

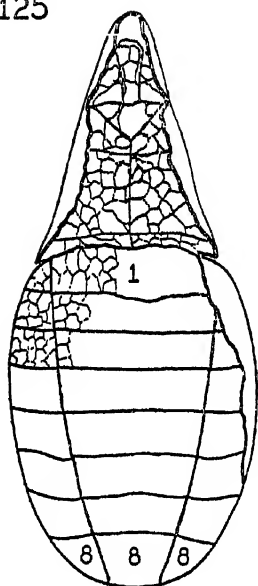
FIGURE 126. *Lissomartus schucherti* (Petrunkévitch). Copy of A. P.'s original figure 63 of the same Monograph, sub *Trigonotarbus*.

FIGURE 127. *Aphantomartus pococki* Pruvost, copy of Pruvost's figure 42 published in 1919.

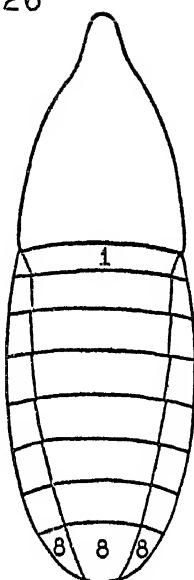
FIGURE 128. *Phrynomartus waechteri* (Guthörl), copy of Guthörl's figure 3a, sub *Eophrynus*.

FIGURE 129. *Hemikreischeria geinitzi* Thevenin, copy of Pruvost's figure 40 published in 1919, slightly reduced.

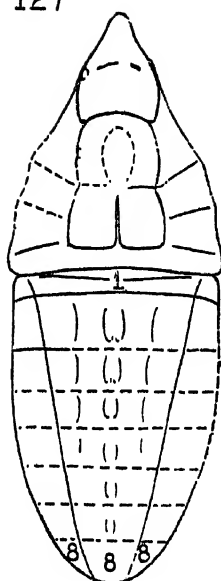
125



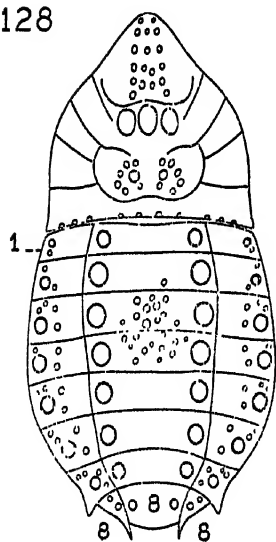
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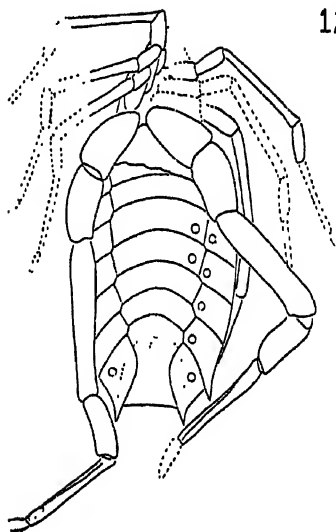


PLATE 42

Goniotarbus tuberculatus n. g., n. sp.

FIGURE 130. Dorsal view of Type specimen No. 31249, x ca.4.

FIGURE 131. Ventral view of the same specimen, x ca.4.

FIGURE 132. Eye tubercle with the eyes of the same specimen, x 22.

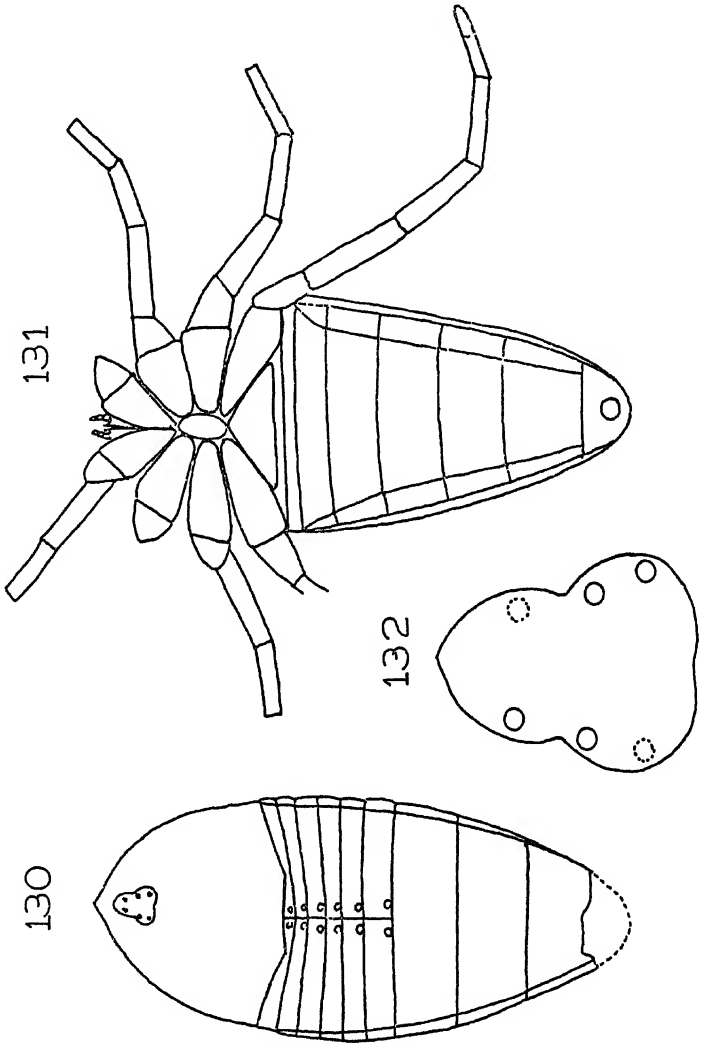


PLATE 43

FIGURE 133. *Goniotarbus tuberculatus* n. sp. Paratype specimen No. 22840. Ventral surface showing coxae and genital region, x 7.

FIGURE 134. *Mesotarbus intermedius* n. g., n. sp. Type, No. 18506. Dorsal surface x 7.

FIGURE 135. Eye tubercle with eyes of type specimen, x 22.

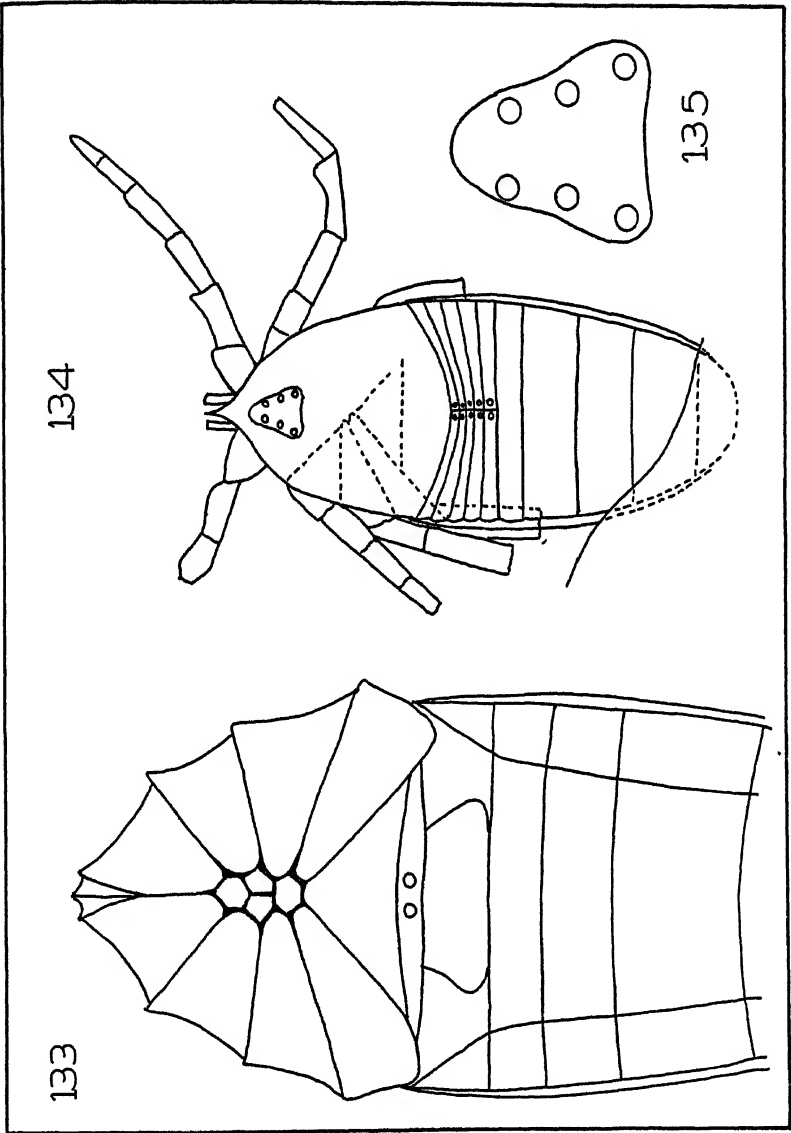


PLATE 44

FIGURE 136. *Centromachus euglyptus* (Peach). Specimen No. 12849,
x 7.

FIGURE 137. *Anthracoscorpio juvenis* Kusta. Specimen No. 39764, x 7.

FIGURE 138. *Archaeoctonus tuberculatus* (Peach). Specimen No. 988,
x 7.

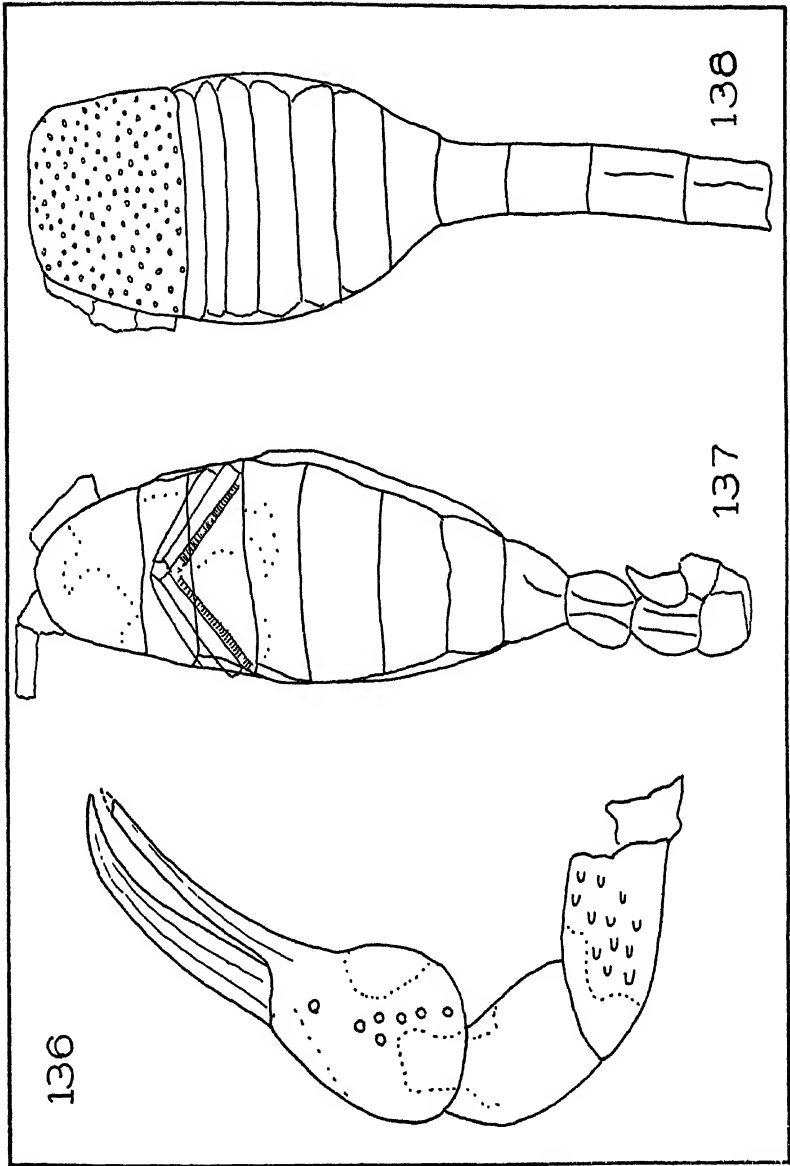


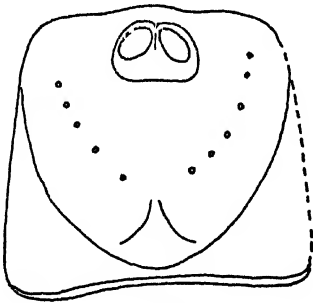
PLATE 45

FIGURE 139. *Lichnophthalmus pulcher* n. g., n. sp. Type specimen No. 39772, x 4.

FIGURE 140. *Europhthalmus longimanus* n. g., n. sp. Type specimen No. 39766, x 2.25.

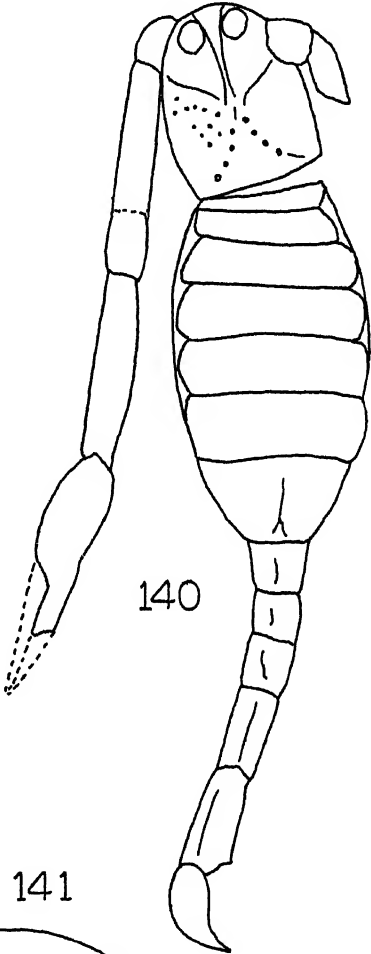
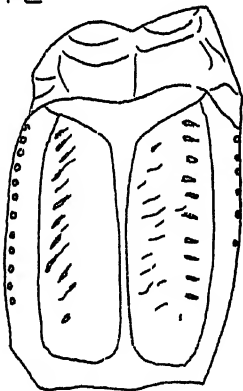
FIGURE 141. The hand of *Europhthalmus longimanus*, Type, x 4.

FIGURE 142. *Europhthalmus* sp. Specimen No. 18603, x 5. Only this segment of the postabdomen is preserved. See text.



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PLATE 46

FIGURE 143. *Typhlopisthacanthus anglicus* n. g., n. sp. Type specimen No. 31261, x 12.

FIGURE 144. *Lichnoscorpius minutus* n. sp. Eyes of type specimen No. 31266, x 80.

FIGURE 145. *Lichnoscorpius minutus* n. g., n. sp. Type specimen No. 31266, x 12.

FIGURE 146. *Typhloscorpius distinctus* n. g., n. sp. Type specimen No. 13909, x 7.

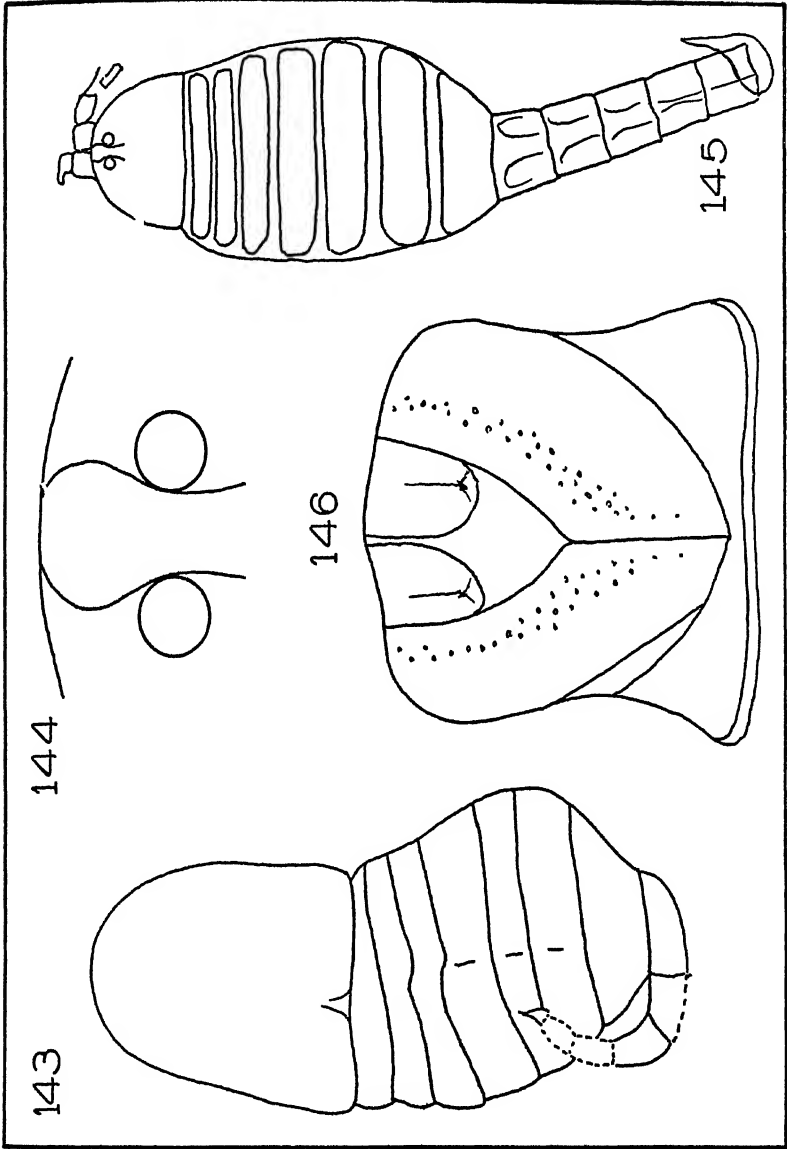


PLATE 47

Compsoscorpius elongatus n. g., n. sp.

FIGURE 147. Dorsal view of type, specimen No. 15862, x 5.

FIGURE 148. Carapace of type specimen, x 22. The left side of the carapace is distorted. Consequently, the lateral eyes are visible only on the right side.

FIGURE 149. A median eye of the Type, x 80.

FIGURE 150. The lateral eyes of the Type, x 80. The thick, curved line is the crest above the eyes.

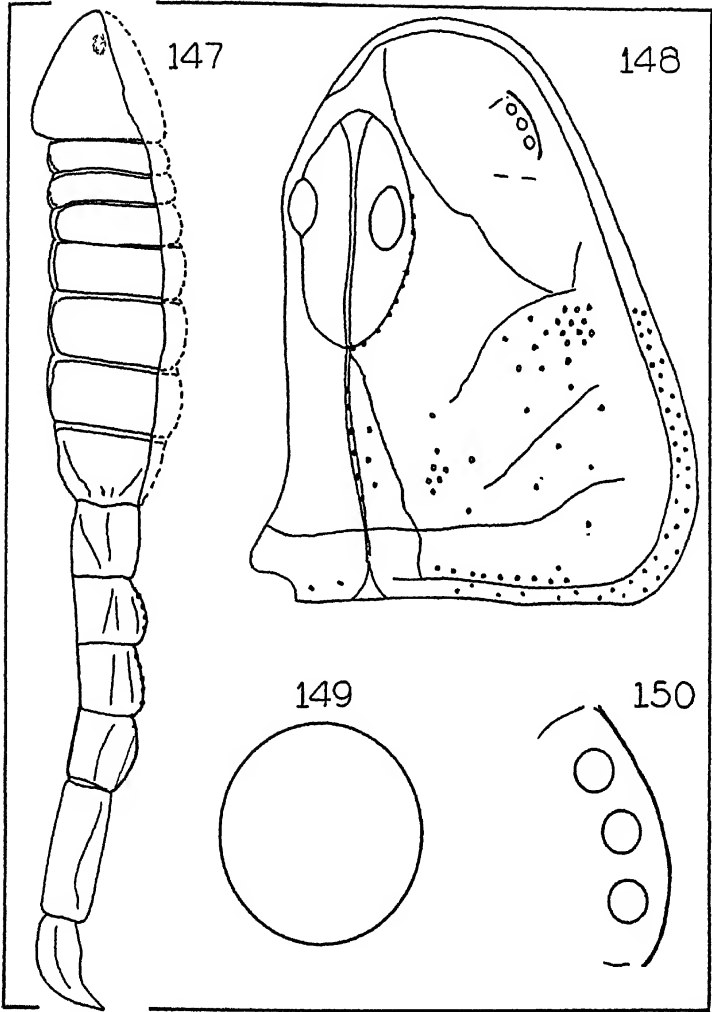


PLATE 48

Compsoscorpius elegans n. g., n. sp.

FIGURE 151. Type specimen No. 788, x 7. This is the specimen described and figured by Pocock as No. 1, figure 7 *Anthracoscorpius burbykovi*. Pocock did not see the eyes and the tail, because they were hidden under extraneous matter.

FIGURE 152. The carapace after cleaning, x 22.

FIGURE 153. A median eye, x 80.

FIGURE 154. The lateral eyes, x 80.

FIGURE 155. The hand of *Palaeomachus anglicus* (Woodward). A copy of Pocock's figure 2a.

FIGURE 156. *Palaeomachus* sp. Specimen No. 13976, x 6.

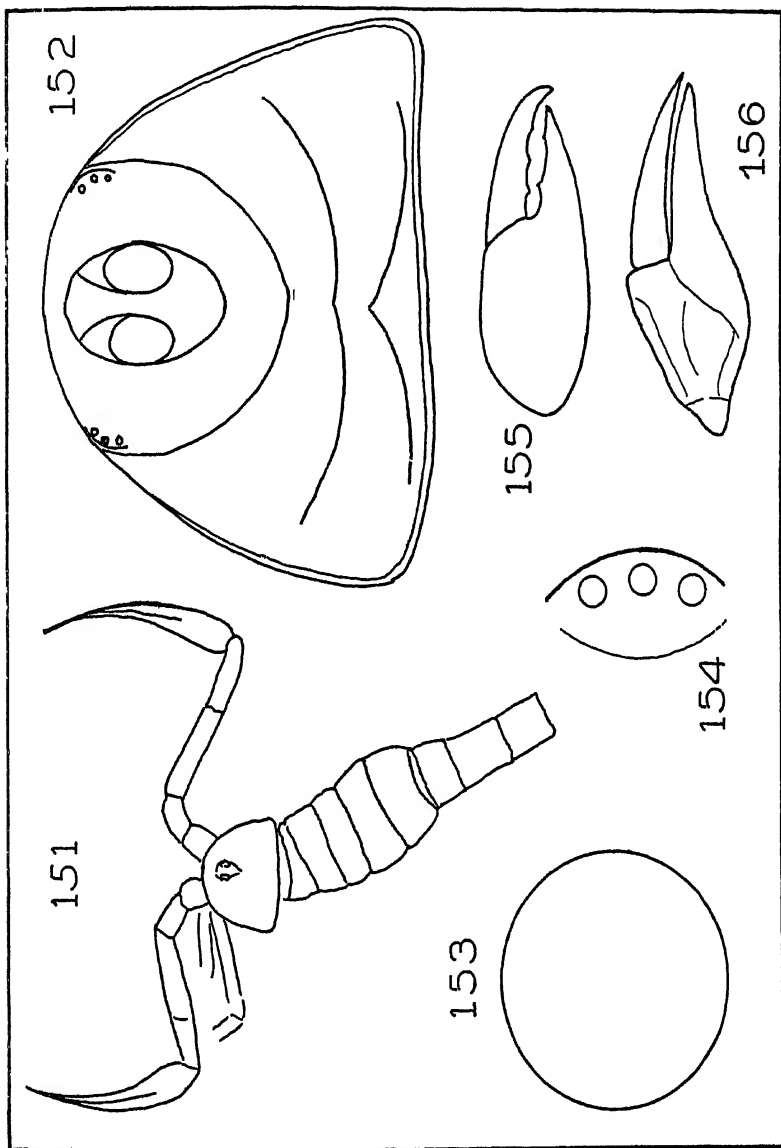


PLATE 49

FIGURE 157. *Geralinura britannica* Pocock, Specimen In. 7912, x 5.5.

FIGURE 158. *Protocteniza britannica* n. g., n. sp. Type. Specimen In. 14015, x 5.5.

FIGURE 159. *Archaeometa nephilina* Pocock, Specimen In. 15863. x 5.5.

FIGURE 160. *Arachnometa tuberculata* n. g., n. sp. Type. Specimen In. 13917, x 5.5.

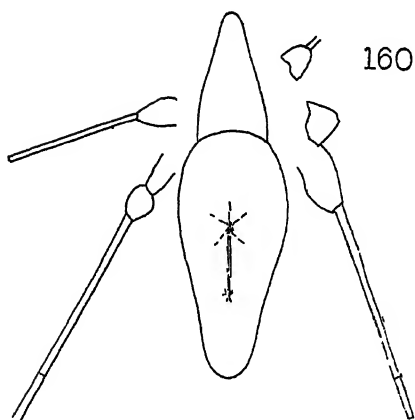
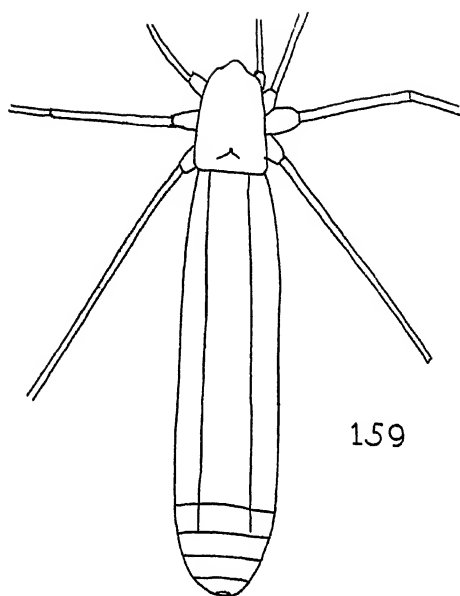
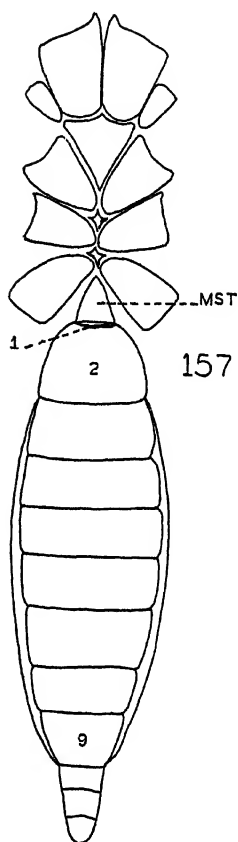


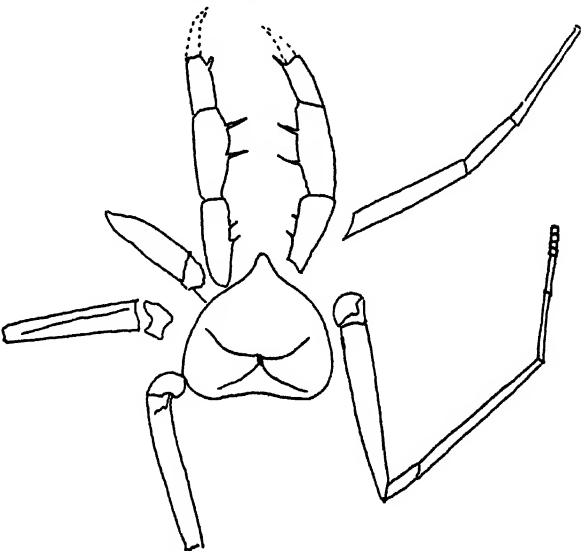
PLATE 50

Graeophonus anglicus Pocock

FIGURE 161. Specimen No. 31257, x 4.

FIGURE 162. Specimen No. 13877, x 7.

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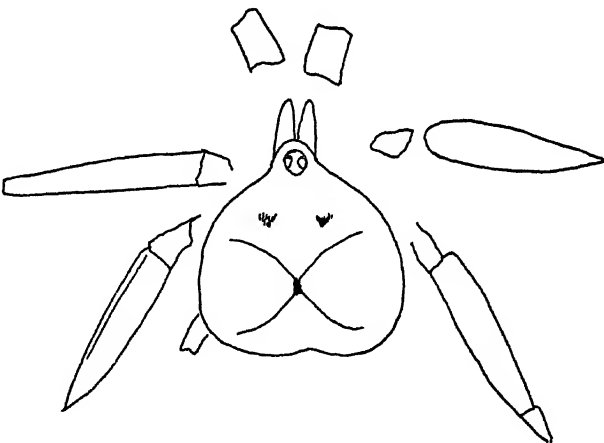


PLATE 51

Curculioides granulatus n. sp.

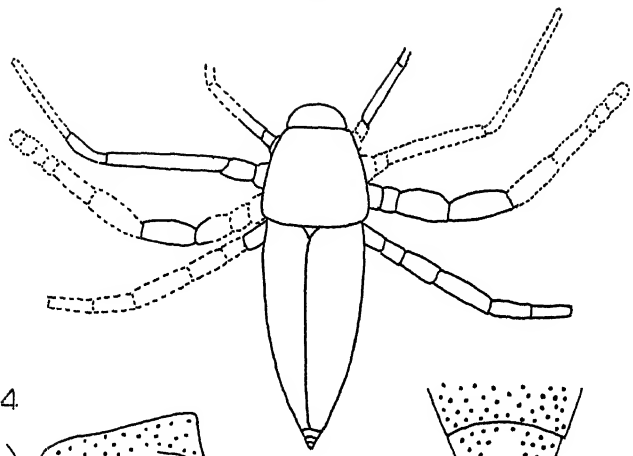
FIGURE 163. Type specimen No. 18592, x 2.25. Dorsal surface.

FIGURE 164. Third right patella of type, x 9.

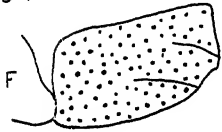
FIGURE 165. Pygidium of type, x 16.

FIGURE 166. Ventral surface of type, x 2.25. Notice the locking apparatus behind the fourth coxae.

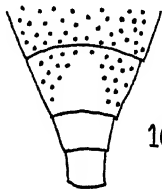
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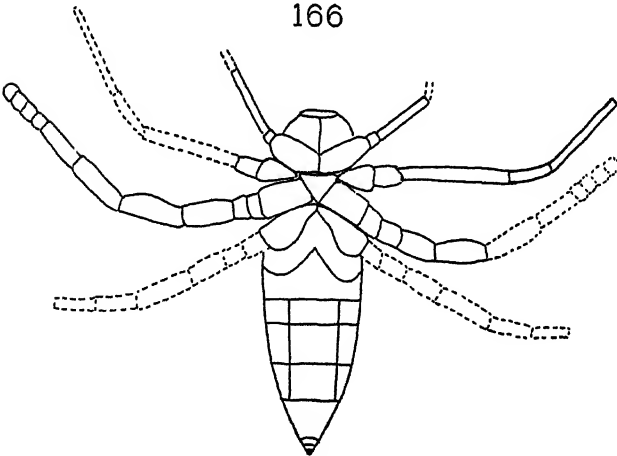


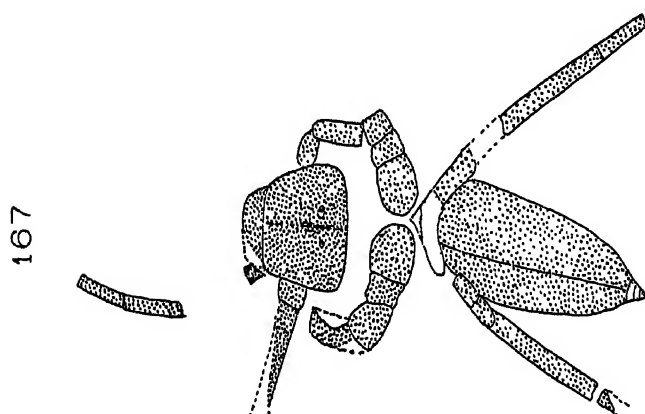
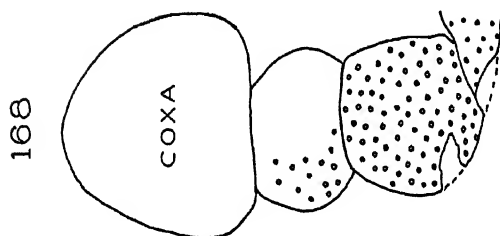
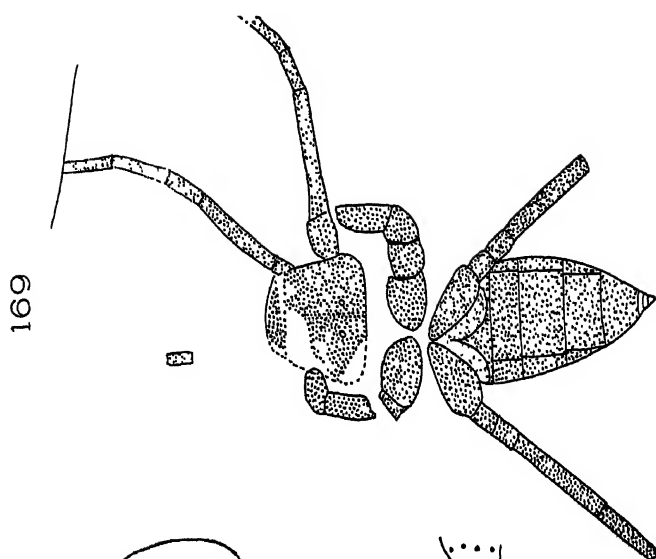
PLATE 52

Curculioides eltringhami n. sp.

FIGURE 167. Type specimen No. 39771. Dorsal surface, $\times 2.15$.

FIGURE 168. Third right leg of type, showing the first three joints, $\times 9$.

FIGURE 169. Ventral view of type, $\times 2.25$.



PLATES 53 - 83

PLATE 53

FIGURE 170. *Palaeophonus nuncius* Thorell and Lindstrom. Copy of original figure showing only the anterior portion of the specimen. Notice the true first tergite under the carapace, its limits outlined by the transverse furrow.

FIGURE 171. *Dolichophonus loudonensis* (Laurie). Copy of original figure, slightly reduced. The species was described under the generic name of *Palaeophonus*.

FIGURE 172. *Palaeophonus caledonicus* Hunter. Copy of Pocock's figure of the type specimen, described by Pocock under the name of *Palaeophonus hunteri*. Slightly reduced.

PLATE 54

FIGURE 173. *Centromachus euglyptus* (Peach). Specimen In. 12849, British Museum. x 6. (See figure 136).

FIGURE 174. *Europhthalmus longimanus* n. g., n. sp. Type, specimen In. 39766. British Museum. Natural size. (See figure 140).

FIGURE 175. *Anthracoscorpio juvenis* Kusta. Specimen In. 39764. x 4.4. British Museum. (See figure 137).

FIGURE 176. *Archaeoctonus tuberculatus* (Peach). Specimen In. 988, x 4.4, British Museum. (See figure 138).

PLATE 55

FIGURE 177. *Lichnophthalmus pulcher* n. g., n. sp. Type, specimen In. 39772, x 4. British Museum. (See figure 139).

FIGURE 178. *Typhloscorpius distinctus* n. g., n. sp. Type, specimen In. 13909. x 4.4. British Museum. (See figure 146).

FIGURE 179. *Europhthalmus* sp? Specimen In. 18603. x 6.3. British Museum. (See figure 142).

FIGURE 180. *Palaeomachus* sp? Specimen In. 13976. x 6. British Museum. (See figure 156).

PLATE 56

FIGURE 181. *Lichnoscorpium minutus* n. g., n. sp. Type specimen In. 31266. x 10. British Museum. (See figure 145).

FIGURE 182. *Typhlopisthacanthus anglicus* n. sp. Type, specimen In. 31261. x 12. British Museum. (See figure 143).

PLATE 57

Composcorpius elegans n. g., n. sp.
Type. Specimen In. 7883. British Museum

FIGURE 183. Specimen as it now appears after cleaning and exposure of carapace and tail. x 4.4. (See figure 151). This is the specimen shown in Pocock's figure 7 under the name of *Anthracoscorpio buthiformis*.

FIGURE 184. Carapace and portion of abdomen of the same specimen, x 12. (See figure 152).

FIGURE 185. A median eye of the same specimen, x 65. To show the circular shape of the eye it was necessary to incline the specimen at a considerable angle. The photograph was made with the aid of a microscope objective 16 (apochromatic) and ocular x 10 (compensating). Strong reflected light was used and the original magnification was 100 diameters. (See figure 153).

PLATE 58

Composcorpius elongatus n. sp.
Type. Specimen In. 15862. British Museum

FIGURE 186. Dorsal view of specimen. x 2.4. (See figure 147).

FIGURE 187. Carapace of the same specimen. x 12. (See figure 148).

FIGURE 188. Lateral eyes of the right side of the same specimen. x 12. (See figure 150).

PLATE 59

FIGURE 189. *Palaeophonus osborni* Whitfield. Type. No. 2257. American Museum of Nat. Hist., New York. x 2.3.

FIGURE 190. *Pleomartus trilobitus* (Scudder), Paratype, specimen No. 37982 (1753d). U. S. National Museum, Washington, D. C. x 4.4. (See figure 58).

FIGURE 191. *Coryphomartus triangularis* (Petrunkévitch). Type, specimen No. 37968, as it appears after cleaning, x 4.4. U. S. National Museum. (See figure 59).

PLATE 60

FIGURE 192. *Anthracomartus völkelianus* Karsch. Type. Copy of Karsch's figure 1, enlarged to be of the same size as the following figure. See text and figure 55.

FIGURE 193. Copy of Haase's figure 9 made by him from a specimen, which he supposed to be the same as the one figured by Karsch. Notice the discrepancies between the two figures.

FIGURE 194. *Pleomartus palatinus* (Ammon). Copy of Ammon's figure described by him under the generic name of *Anthracomartus*. Slightly enlarged. The lines shown belong partly to the ventral surface. See the text for explanation.

PLATE 61

Cryptomartus hindi (Pocock)
Specimen In. 13955. British Museum

FIGURE 195. Dorsal view of specimen, x 3.7. (See figure 64).

FIGURE 196. Ventral view of the same specimen, x 3.7. (See figure 65).

PLATE 62

FIGURE 197. *Cryptomartus hindi* (Pocock). Specimen In. 13955. Inside view of crest. x 4.25. British Museum. (See figure 67).

FIGURE 198. *Cryptomartus hindi* (Pocock). Genital region of the same specimen, x 10.3. (See figure 71).

FIGURE 199. *Cryptomartus hindi* (Pocock). End of first left tarsus with claw. Specimen In. 18338. x 33. British Museum. (See figure 70).

FIGURE 200. *Cryptomartus priesti* (Pocock). Specimen In. 15858. Inside view of crest, x 13. British Museum. Compare with figure 77.

FIGURE 201. *Cryptomartus priesti* (Pocock). Plastic clay cast of specimen In. 7893, viewed from in front, x 6.6. British Museum.

FIGURE 202. *Cryptomartus priesti* (Pocock). Plastic clay cast of specimen, In. 15858 of the British Museum, in side view. x 6.6.

PLATE 63

Cryptomartus priesti (Pocock)

FIGURE 203. Dorsal view of Specimen In. 7893 of the British Museum, x 3.3. (See figure 74).

FIGURE 204. Specimen In. 31264 of the British Museum, x 3. (Piece *a*). Compare with figure 41.

FIGURE 205. Specimen In. 31264, Piece *b*, x 3. The photograph shows the ventral surface of the posterior end of the abdomen after removal of the matrix of which a piece is left in front, to show the tergites.

PLATE 64

Cryptomartus priesti (Pocock)

FIGURE 206. Dorsal view of female, Specimen In. 31268. x 4. British Museum. Compare with figure 53.

FIGURE 207. Ventral view of same specimen. x 4. (See figure 76).

FIGURE 208. Specimen In. 31237 of the British Museum. Cheliceral and pedipalpal coxae. x 12. (See figure 29).

FIGURE 209. Specimen In. 31268 of the British Museum. Anterior sternal region showing cheliceral coxae. x 13.

FIGURE 210. Specimen In. 7893 of the British Museum. Anterior visceral depression, visible on the ventral surface of the abdomen. x 6.

PLATE 65

FIGURE 211. *Cleptomartus plautus* n. sp. Specimen In. 15857. Androtype. View of dorsal surface x 3.9. British Museum.

FIGURE 212. Ventral surface of the same specimen, x 3.9.

FIGURE 213. *Cryptomartus priesti* (Pocock). Specimen In. 22842 of the British Museum. Genital region showing lungs and apodemes, x 12.

FIGURE 214. *Cryptomartus priesti* (Pocock). Specimen In. 31268 of the British Museum. Female. Genital region showing also lungs and apodemes. x 16.

FIGURE 215. *Cryptomartus priesti* (Pocock). Male, Specimen In. 31237 of the British Museum. Genital region x 10.

PLATE 66

Cleptomartus plautus n. g., n. sp.

Type. Female. Specimen In. 15896. British Museum

FIGURE 216. Dorsal surface. x 5.4. (See figure 81).

FIGURE 217. Ventral surface. x 5.4. Compare with figure 89.

PLATE 67

FIGURE 218. *Cleptomartus planus* n. sp. Type, Specimen In. 7918. Dorsal view of specimen, x 4.7. British Museum. (See figure 90).

FIGURE 219. Ventral view of same specimen, x 4.7. (See figure 91).

FIGURE 220. Same specimen. Second joint of chelicerae shown in front view. x 13.

FIGURE 221. *Cleptomartus plautus* n. g., n. sp. Type. Female. Specimen In. 15896. Cheliceral region x 12. British Museum.

FIGURE 222. *Cleptomartus plautus*, specimen In. 7916. Cheliceral region x 12. British Museum. (See figure 30).

FIGURE 223. *Cleptomartus plautus* n. g., n. sp. Type. Female. Specimen In. 15896. Genital region x 10. British Museum.

FIGURE 224. *Cleptomartus plautus*, specimen In. 7916. Female. Genital region x 8. British Museum. (See figure 88).

FIGURE 225. *Cryptomartus priesti* (Pocock). Specimen In. 7893 of the British Museum. Second joint of chelicerae, x 12.

PLATE 68

FIGURE 226. *Cryptomartus priesti* (Pocock). Male. Specimen In. 22842. x 5. British Museum.

FIGURE 227. *Cleptomartus plautus* Specimen In 18336 of the British Museum. Genital region x 8.

FIGURE 228. *Xiphosura (Limulus) polyphemus* (Linnaeus). Inside view of the coxo-sternal region after removal of all soft tissues. From a preparation made by the author. (See figure 28).

PLATE 69

Plesiosiro madeleyi Pocock

FIGURE 229. Dorsal view of specimen In. 7922. Magnification ca. x 3.7.

FIGURE 230. Ventral view of the same specimen at the same magnification.

PLATE 70

Plesiosiro madeleyi Pocock

FIGURE 231. Plastic clay cast of Pocock's paratype, specimen In. 18341 of the British Museum. x 5.

FIGURE 232. Specimen In. 7922. Ventral surface of abdomen x 10.4. British Museum. (See figure 101).

PLATE 71

Plesiosiro madeleyi Pocock

FIGURE 233. End of first left leg of specimen In. 7922, showing metatarsus and six-jointed tarsus. x 12.3. British Museum. (See figure 96).

FIGURE 234. End of third right leg of specimen In. 18341, showing metatarsus and four-jointed tarsus. x 12. British Museum. (See figure 98).

FIGURE 235. Ventral surface of specimen In. 7923, showing cheliceral coxae with the typical foramina. x 12. British Museum. (See figure 25).

FIGURE 236. Carapace of specimen In. 7922. x 12. British Museum.

FIGURE 237. Eyes of specimen In. 7922. x 55. British Museum. (See figure 102).

PLATE 72

Goniotarbus tuberculatus n. sp.

FIGURE 238. Paratype In. 15864. View of dorsal surface x 4.4. British Museum.

FIGURE 239. Paratype In. 22840. View of ventral surface x 4.4. British Museum. Compare with figure 133.

PLATE 73

Goniotarbus tuberculatus n. g., n. sp.

FIGURE 240. Type, specimen In. 31249, Piece *a*. view of dorsal surface x 2.3. British Museum. (See figure 130).

FIGURE 241. Same specimen, view of ventral surface x 2.3 (Piece *b*). (See figure 131).

FIGURE 242. *Mesotarbus intermedius* n. g., n. sp. Type, specimen In. 18506. View of dorsal surface x 4.4. British Museum. (See figure 134).

PLATE 74

Anthracosiro woodwardi Pocock Specimen In. 1552 of the British Museum

FIGURE 243. Piece *a* showing dorsal surface x 3.7. (See figure 112).

FIGURE 244. Piece *b* showing ventral surface x 3.7.

PLATE 75

Anthracosiro woodwardi Pocock

FIGURE 245. Pocock's paratype, In. 1554, after cleaning. Dorsal surface (Piece *a*) x 3.7. British Museum. (See figure 113).

FIGURE 246. Same specimen, Piece *b*. Ventral surface after cleaning. (See figure 114).

FIGURE 247. Specimen In. 1552. Piece *a*. Connection between carapace and abdomen, showing radiating dorsal longitudinal muscle fibers. x 12. British Museum. (See figure 40).

PLATE 76

FIGURE 248. *Anthracosiro woodwardi* Pocock. Pocock's paratype In. 1554 showing genital region after cleaning. x 12. British Museum. (See figure 115).

FIGURE 249. *Anthracosiro fisheri* Pocock. Electrocast of specimen In. 14629. x 6. British Museum.

PLATE 77

Trigonotarbus johnsoni Pocock

FIGURE 250. Dorsal view of specimen In. 31240. x 10. British Museum.

FIGURE 251. Ventral view of specimen In. 7895. x 11.5. British Museum.

PLATE 78

Trigonotarbus johnsoni Pocock

FIGURE 252. Dorsal view of specimen In. 15897. x 6.7. British Museum (See figure 106).

FIGURE 253. Ventral view of specimen In. 15897. x 6.7. British Museum. (See figure 111).

FIGURE 254. Anterior end of carapace with eyes. x 5. Specimen In. 31240. British Museum. (See figure 107).

FIGURE 255. Anterior end of carapace with eyes. x 6. Specimen In. 31243. British Museum. The eyes of this specimen are fossilized with lenses in toto (convex).

FIGURE 256. Specimen In. 31254 of the British Museum, showing two lungs of one side, x 30.

FIGURE 257. Specimen In. 13911 of the British Museum. Anterior end of abdomen, showing the triangular first sternite. The book-lungs which should be visible on sternites two and three are missing, having been broken off. x 10.

PLATE 79

FIGURE 258. *Eophrynus varius* n. sp. Type, specimen In. 39767. x 3.5. British Museum. (See figure 110).

FIGURE 259. *Pleophrynus ensifer* Petrunkevitch. Dorsal view of type, No. 14873 of the Illinois State Museum. x 2.

PLATE 80

FIGURE 260. *Archaeometa nephilina* Pocock. Specimen In. 15863 of the British Museum, x 3.9. (See figure 159).

FIGURE 261. *Arachnometa tuberculata* n. g., n. sp. Type. Specimen In. 13917 of the British Museum, x 5. (See figure 160).

FIGURE 262. *Protocteniza britannica* n. g., n. sp. Type. Specimen In. 14015 of the British Museum, x 6.7. (See figure 158).

FIGURE 263. *Gracophonus anglicus* Pocock, specimen In. 13877, dorsal view, x 4.7. British Museum.

PLATE 81

FIGURE 264. *Gracophonus anglicus* Pocock, specimen In. 13877, ventral view, x 4.7. British Museum.

FIGURE 265. *Geralinura britannica* Pocock, specimen In. 7912, dorsal view, x 3.7. British Museum.

FIGURE 266. *Curculioides granulatus* n. sp. Type, specimen In. 18592 of the British Museum. Ventral view x 2.3. (See figure 166).

PLATE 82

FIGURE 267. *Curculioides granulatus* n. sp. Type, specimen In. 18592 of the British Museum. Dorsal view x 2.3. (See figure 163).

FIGURE 268. *Graeophonus anglicus* Pocock, specimen In. 31257 of the British Museum, x 2.

FIGURE 269. *Curculioides ansticii* Pocock, Paratype, In. 7885 of the British Museum, x 3.3.

PLATE 83

Curculioides eltringhami n. sp.

Type, specimen In. 39771. British Museum

FIGURE 270. Piece *a* showing dorsal surface x 2.2. (See figure 167).

FIGURE 271. Piece *b* showing ventral surface x 2.2. (See figure 169.)



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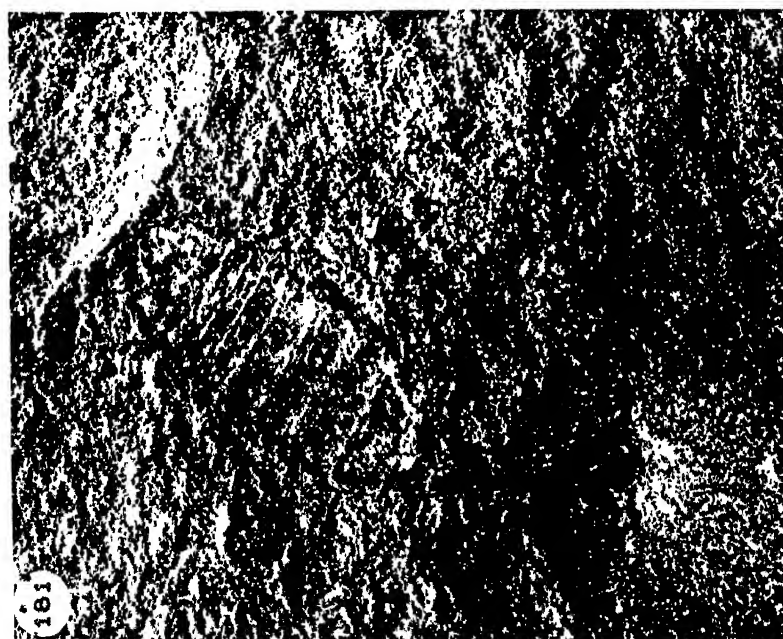
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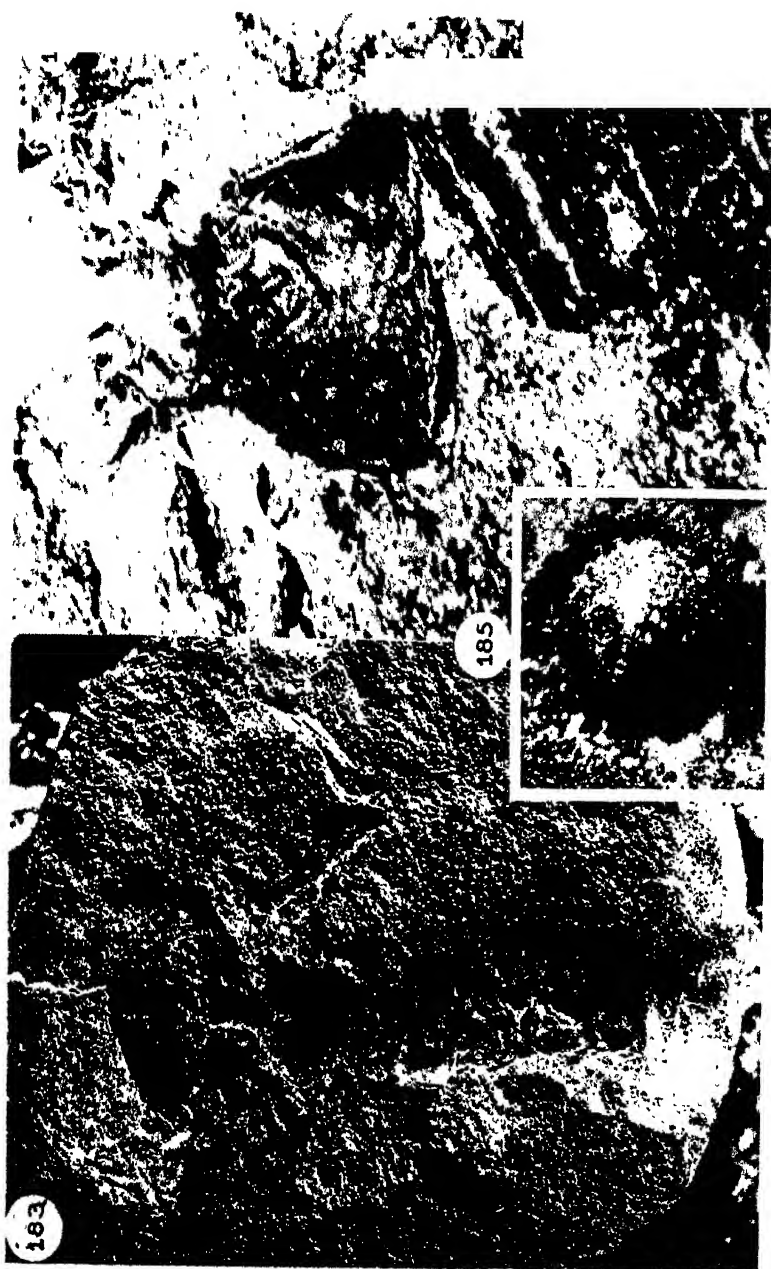


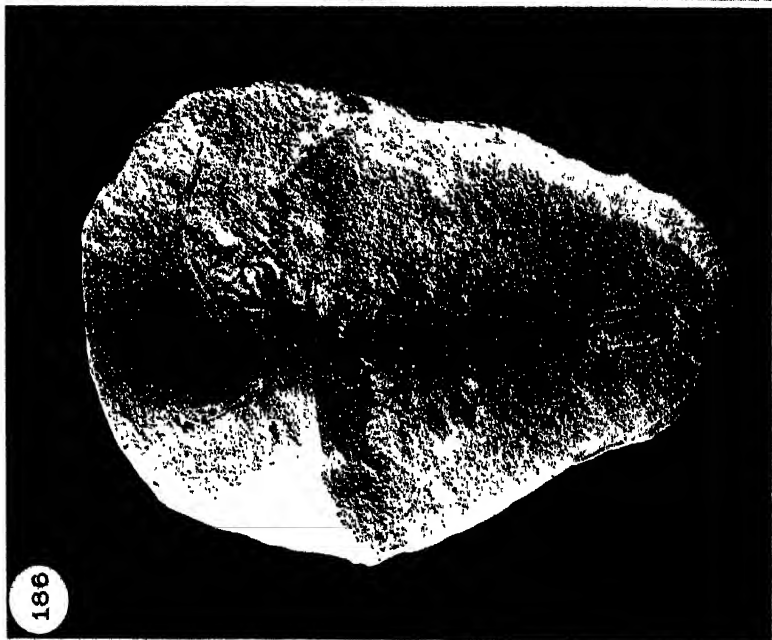
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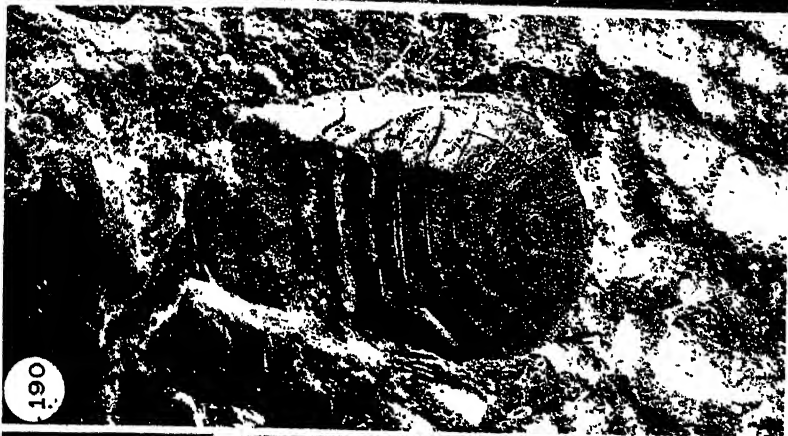




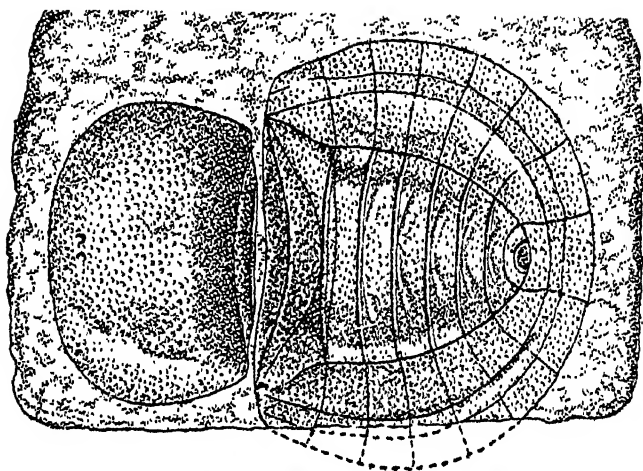




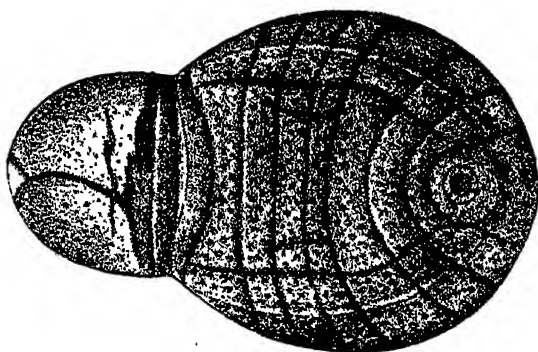




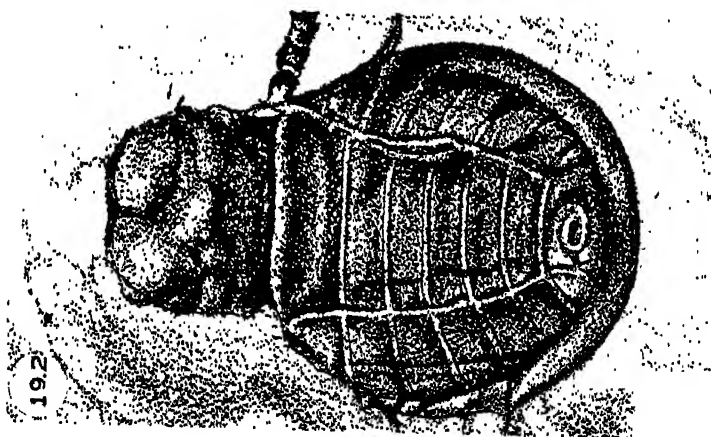
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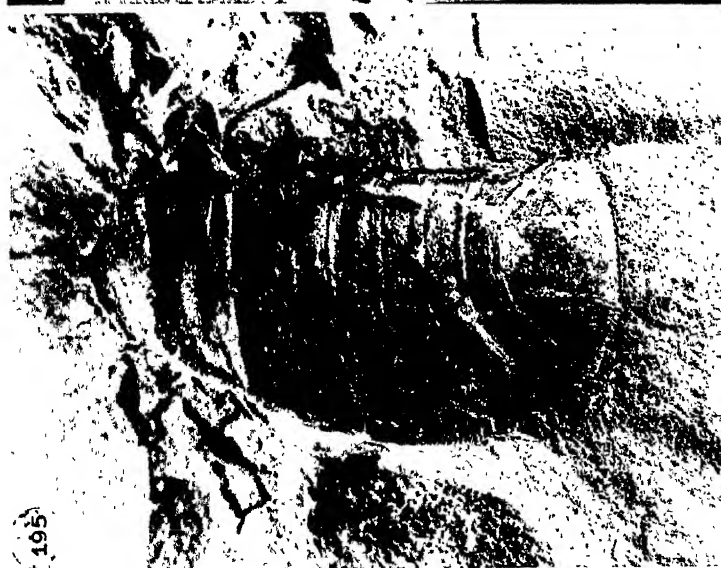


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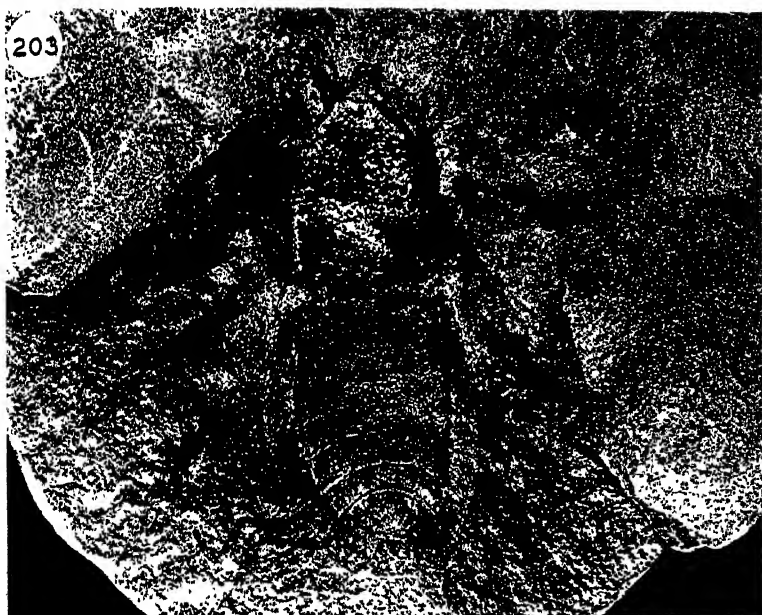


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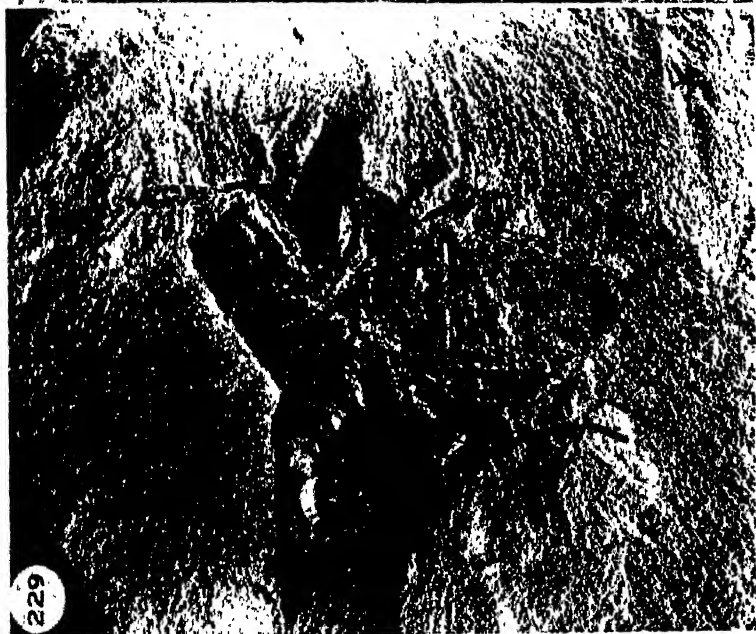


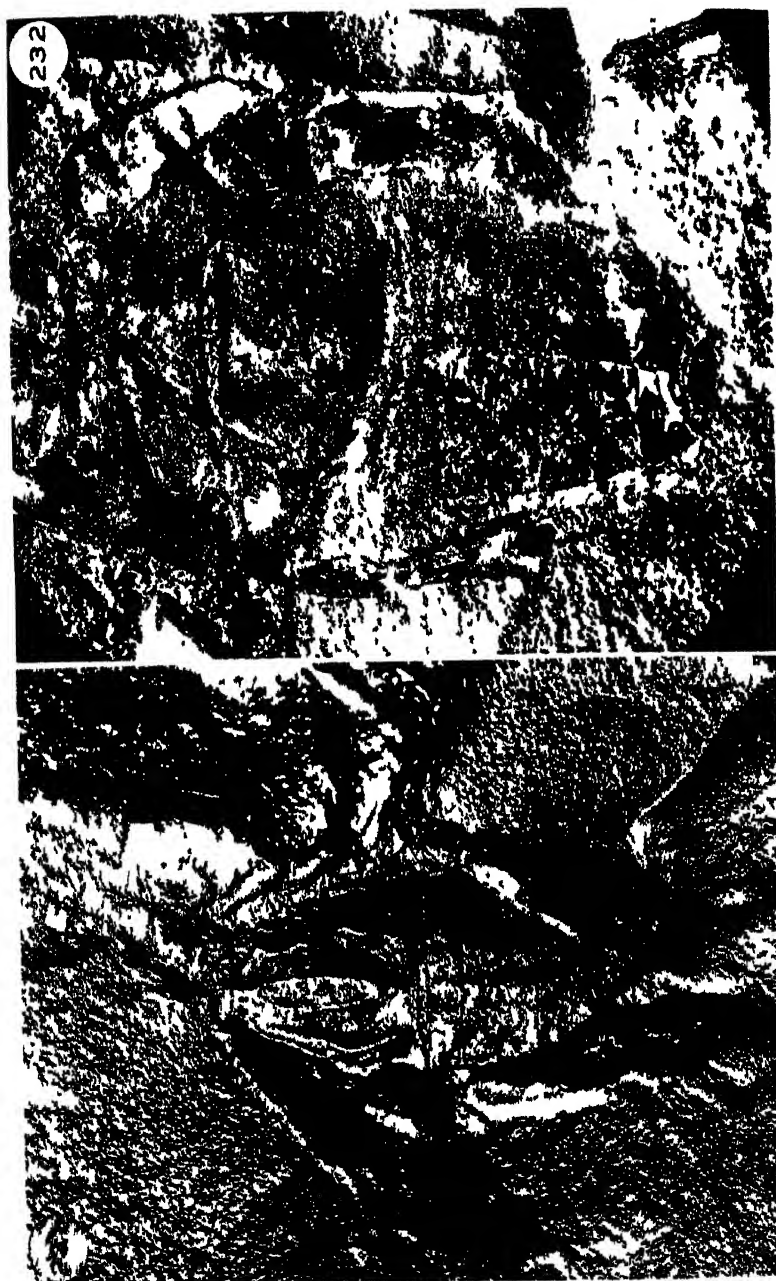




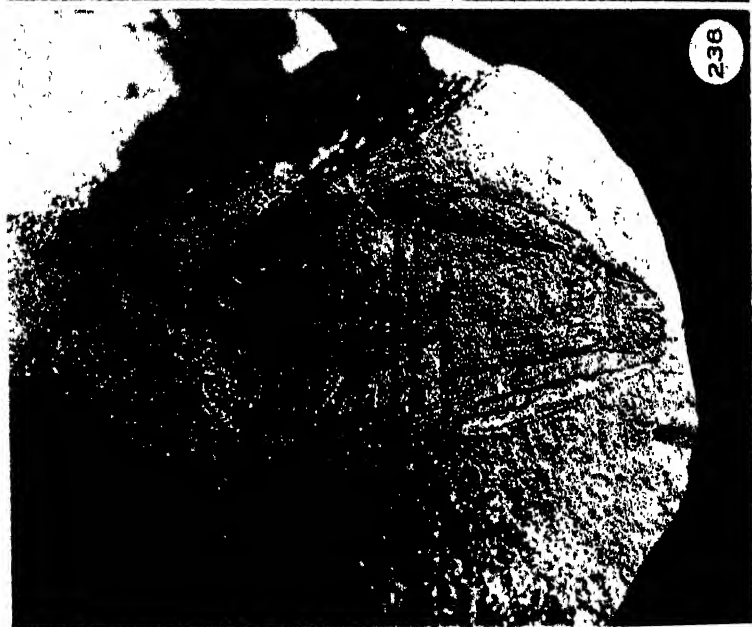








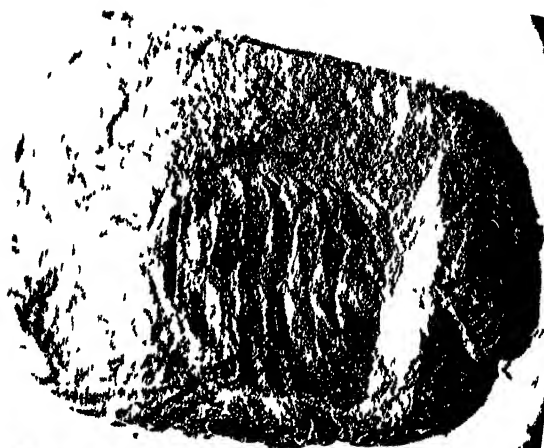




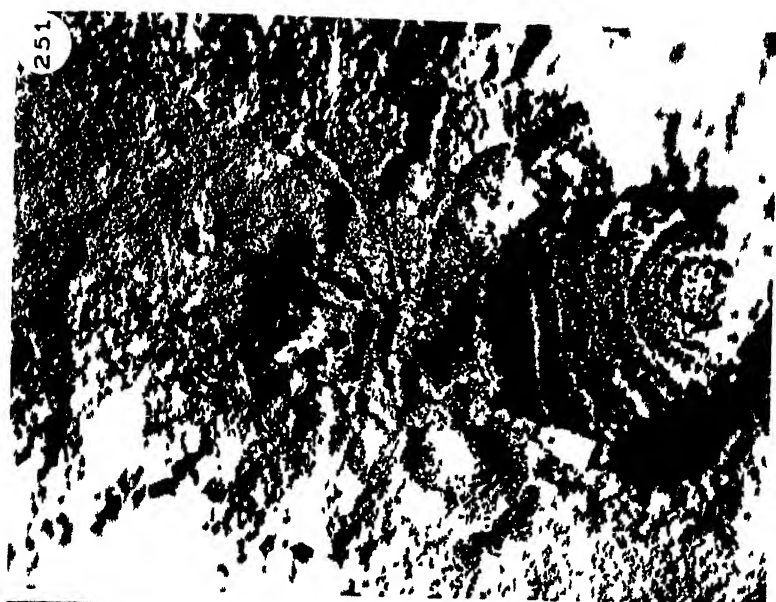




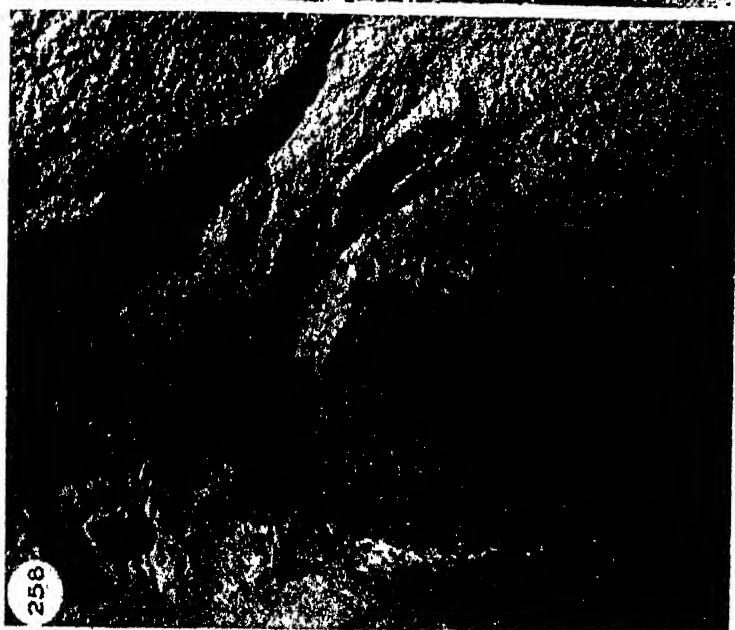


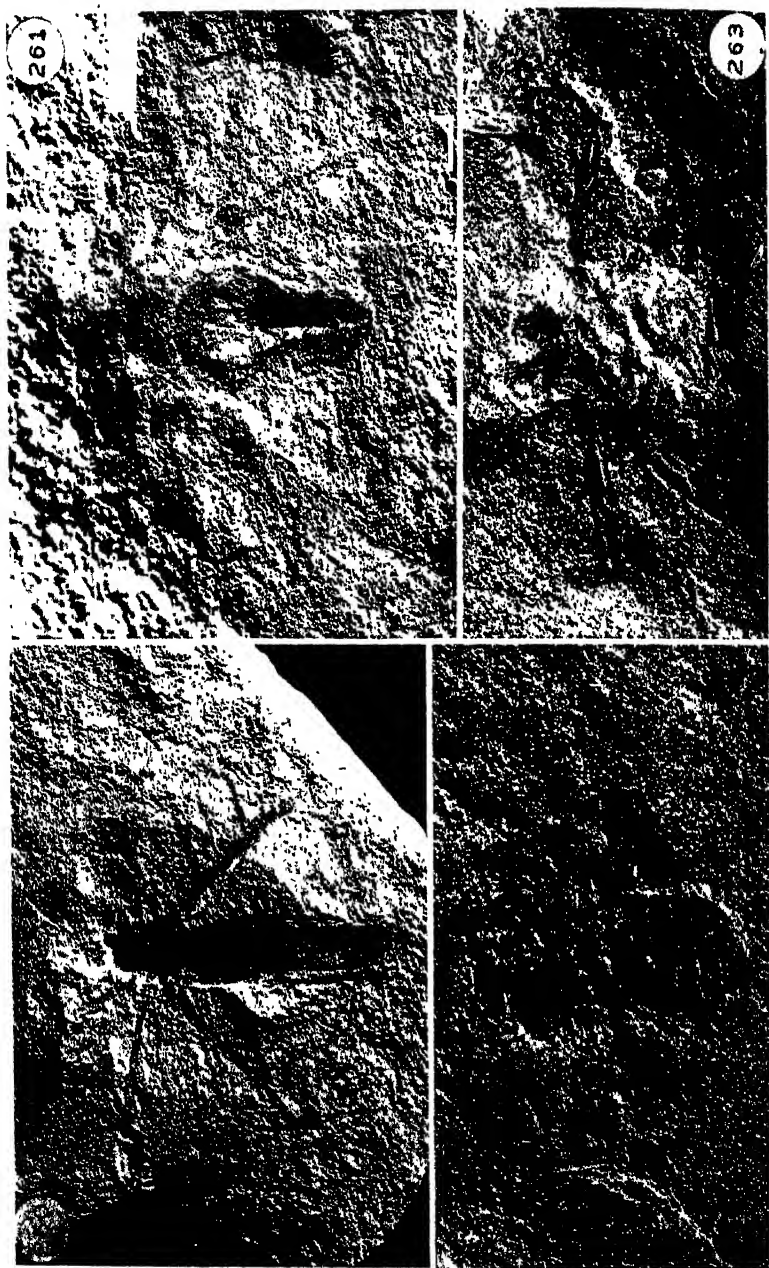


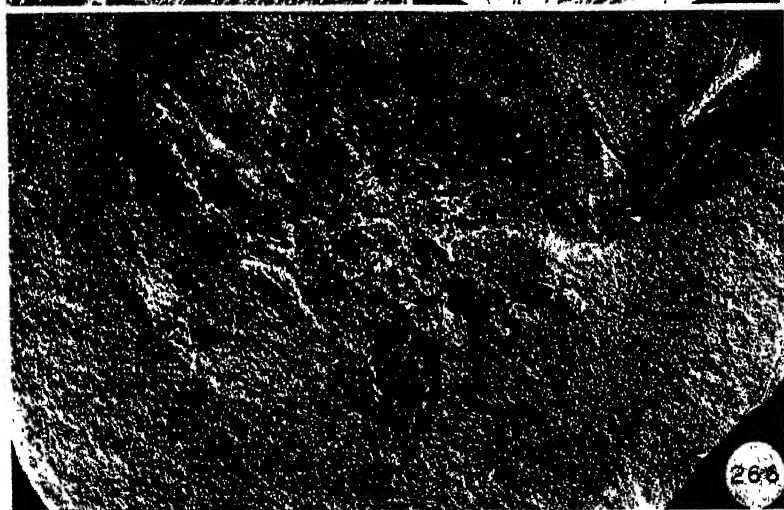
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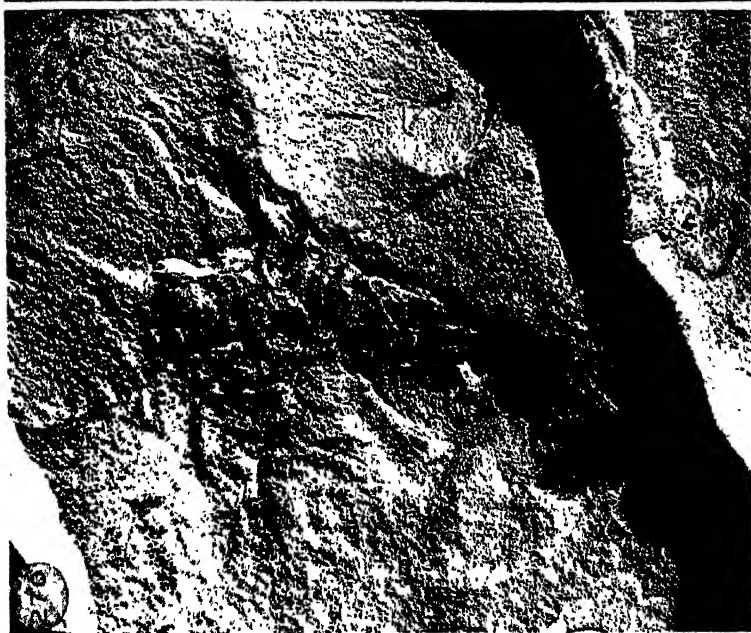
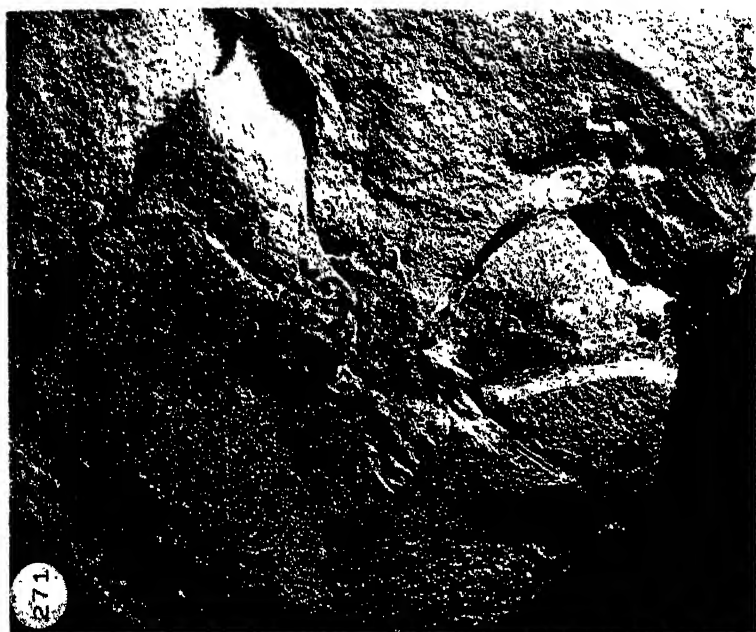












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* Owing to an unfortunate oversight this genus appears only in the key on page 142. It was proposed by me in 1913 for a species from the Pennsylvanian of Mazon Creek, Illinois.

Genus *Trigonoscorpio* Petrunkevitch, 1913

Type *T. americanus* Petrunkevitch, Trans. Conn. Acad., Vol. 18, p.47, Figure 10, Plate IV, Figures 17 and 18.

LIST OF DESCRIBED SPECIES OF PALAEOZOIC ARACHNIDA

Synonyms in italics. Figures in black type refer to pages in this paper. Figures in brackets refer to the number under which the title of the paper is listed in the References and the page of the paper, on which the species is described.

<i>affinis Anthracomartus</i>	(23, p. 39)
<i>alticeps Polyochera</i>	p.286; (111, p. 40)
<i>americanus Trigonoscorpio</i>	p.iii ; (93, p. 47)
<i>anglicus Eoscorpium</i>	p.137; (148, p. 58)
<i>anglicus Graephonus</i>	p.271; (111, p. 32)
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